KARYOTYPIC, GENIC, AND MORPHOLOGICAL VARIATION IN THE LIZARD *SCELOPORUS OLIVACEUS*

A Dissertation

by

ROBERT HAYES DEAN

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ABSTRACT

Karyotypic, Genic, And Morphological Variation In The Lizard *Sceloporus olivaceus* (December 1984)

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Sceloporus olivaceus, an iguanid lizard of the *spinosus* group ranges throughout Texas and northeastern Mexico and was subjected to karyotypic, genic, and morphological analyses. Karyotypes were examined in 13 sample localities throughout its range and were found to be invariate. Electrophoretic analysis was used to assay 17 presumptive gene loci in 12 sample localities of the species supporting previous studies of population structure. These data indicate a large effective population size and little genetic differentiation such that there were few geographic affinities. Low levels of heterozygosity may be indicative of a recent past bottleneck experienced by the species. Morphological analysis revealed a narrow range of variation with no evidence of area effects. In both electrophoretic and morphological data sets, peripheral samples appeared to be most divergent.

Statistical tests among data sets indicated congruency at the 90% confidence level. This may indicate further evidence of a recent

past bottleneck.

The electrophoretic analysis was also used to determine the relationship of *S. olivaceus* and *S. cautus* (*undulatus* group). *S. cautus* was found to be close to *S. olivaceus* and may be a member of the *spinosus* group.

DEDICATION

This is dedicated to my best friend, a young lady who lifts my spirits and holds my heart, Krisser Chenicek.

ACKNOWLEDGEMENTS

This dissertation represents the culmination of several years of hard work and the accomplishment of one of my goals in life. Its completion was greatly facilitated by the combined efforts of many people to whom I will be forever grateful. They provided the drive to succeed, the energy to continue, the knowledge to understand, and, most of all, lasting friendships. I will attempt to acknowledge those who, in some way, contributed to this effort. Hopefully, those friends I fail to mention will understand it is due to poor memory and not a purposeful slight.

My career as well as this study has benefitted immeasurably due to the efforts of my Committee Chairman, James R. Dixon. He spurred my interest in herpetology and evolutionary biology, and, most important, he made me think. Doc has been a major influence in the development of each of his graduate students and I am grateful to have been associated with him. To both him and his wife, Mary, I am indebted and I value their friendship. Thank-you, Doc, for your friendship and for teaching me.

Thanks are in order for the other members of my graduate committee. John W. Bickham provided laboratory space, materials, and equipment for karyotyping. Further, John is a good friend who continually amazes me with his productivity. It has been an immense pleasure to be associated with him and his family. Thank-you John for your efforts and guidance.

John D. McEachran more than anything else provided stimulating thought. I value his friendship and his assistance throughout my

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Other friends and colleagues who provided encouragement, support, or aid in the field include: Steve Branstetter, Paisley Cato, Stuart Calhoun, Russ Cohen, Jim Derr, Mary Dixon, Toby Dixon, Mark Engstrom, Deborah Gust, Brian Hanks, Fred Hendricks, Jerry Johnson, Tom Lee, Eddie Mathison, Karen McBee, Mike McCoid, Tom Miyake, Mike Retzer, Duke Rogers, Jack Sites, Steve Smith, Mike Smolen, and Prilla Tucker.

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My family has been a continual source of encouragement and support and to them I express my heartfelt thanks. Lastly, I think it only fitting that thanks and appreciation go out to all those Rusty lizards who sacrificed themselves in the name of science. Thanks.

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INTRODUCTION

The iguanid lizard genus *Sceloporus* was described by Cope (1900) as "an excellent *piece de resistance*" for those who do not believe in speciation. The genus is one of the largest and most recently evolved reptilian groups of the New World (Smith, 1939). Smith further notes that the genus is accompanied by great variability with frequent intergradation through chains of subspecies; thus the taxonomy is poorly understood. This has resulted in several phylogenies which, in general, disagree in the placement of species within the species groups established by Smith (1939). Approximately 60 species in 15 species groups have been recognized based on morphology (Smith, 1939); karyology (Lowe, Cole, and Patton, 1967; Cole, 1970, 1971a, 1971b, 1972, 1978; Hall, 1971, 1973); behavior (Bussjaeger, 1971; Carpenter, 1967, 1983; Purdue and Carpenter, 1972a, 1972b; Hunsaker, 1962); and serology (Guttman, 1970). Larsen (1973) and Larsen and Tanner (1974, 1975) used osteology and other characters collectively to construct their phylogeny of the genus.

The most notable in-depth evolutionary studies of a sceloporine species to date are Sites (1980, 1982, 1983) and Sites and Greenbaum (1983). They studied chromosomal, allozymic, and morphological variation in *Sceloporus grammicus*, a wide ranging species inhabiting a wide variety of habitats and possessing six chromosomal morphs. Sites (1980) used three cytotypes of *S. grammicus* to test the deme

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This dissertation follows the style of the journal Evolution.

size models (White, 1968, 1969; Bush, 1975; Hall, 1973) and the canalization model (Bickham and Baker, 1979) of chromosomal evolution. The deme size models of chromosomal evolution suggest that rearrangements are causally related to speciation with the rearrangements being fixed by random genetic drift. The rearrangements result in cytotypes which may be reproductively isolated from each other and fixation of the rearrangement can occur in species with high inbreeding in small demes. The occurance of fixed rearrangements, either by stasipatric or parapatric means, allows the new cytotype to expand its range resulting in phyletic speciation or the formation of two species. The canalization model proposes that selection of new rearrangements is the determining force and that chromosomal divergence is not causally related to speciation. As a lineage invades a new adaptive zone, an optimum karyotype is achieved and once stabilized becomes fined tuned by Robertsonian changes. In other words, the karyotype is adaptive and subjected to natural selection.

Important implications of chromosomal evolution were analyzed in *S. grammicus* by documenting the distribution of the cytotypes which could determine concordance between cytotype and habitat perhaps illustrating origins of the cytotypes by some selective force. Further, distributional data could provide information concerning the derivation of the chromosomal morphs by allopatric isolation, intergradation through broad transition zones, parapatric contact zones, or reproductive isolation in sympatry. Secondly, Sites searched for phenotypic characters by which the different cytotypes

might be identified as were found by Schmidly (1973) and Davis and Baker (1974) in the Brush mouse *Peromyscus boylii* and cryptic species of the bat genus *Macrotus*, respectively. Morphological analyses were used to identify past populational bottlenecks and to determine any congruent relationship between phenotype and cytotype. Thirdly, electrophoretic analysis was used to identify structural gene loci which might distinguish cytotypes (demonstrating congruence between genic variation and chromosomal variation) as well as to determine past populational events.

The results of Sites (1980, 1982, 1983) and Sites and Greenbaum (1983) are summarized below. The three cytotypes of *S. grammicus* were characterized by chromosomal polymorphisms which included pericentric inversions and Robertsonian rearrangements (fissions and fusions). The frequency and distribution of the polymorphisms indicate that the heterozygotes have not reduced fitness or viability and are probably not responsible for the genetic divergence and speciation of the group. The three cytotypes were morphologically very similar suggesting that chromosomal and morphological evolution are not related, thereby disputing Wilson's model of correlated rates of chromosomal and morphological evolution (Wilson, 1976; Wilson *et al.*, 1974a, 1974b, 1975, 1977; Bush *et al.*, 1977; Levin and Wilson, 1976; Prager and Wilson, 1975). The morphological continuity within and among the cytotypes is suggestive of extensive gene flow despite chromosomal divergence. Allozymic analysis revealed macrogeographic conservatism with the populations sharing the same alleles. Further, genetic similarity and distance values and shared alleles at most

loci indicate that chromosomal differences are not reducing gene flow between the cytotypes. High levels of heterozygosity imply that the more derived cytotypes did not originate via recent bottlenecks and extensive inbreeding. Low genetic distance and Fst values are indicative of high levels of outcrossing and large effective population size (Ne) such that chromosomal evolution in *S. grammicus* could not have occurred by models of chromosomal transilience (Templeton, 1980) or stasipatric speciation. The data suggest that allopatric isolation is more effective than chromosomal rearrangements in promoting genetic differentiation and that gene flow among the cytotypes is extensive such that chromosome evolution in *S. grammicus* may be deterministic as opposed to stochastic.

Sites' study and results raise questions concerning evolution in the genus *Sceloporus*. Is evolution in *S. grammicus* typical for the genus? In other words, have other species of *Sceloporus* evolved by patterns similar to *S. grammicus*? Larsen and Tanner (1975) note that the genus exemplifies patterns of convergence, divergence, parallelism, drift, allopatry, adaptive radiation, and centrifugal speciation and conclude that the genus recently speciated in an explosive manner. Are the modes of speciation and the phylogeny of the genus correlated? Analysis of evolutionary trends of species and species groups may reflect some phylogenetic relationship. Is there data set congruence within species or species groups of the genus? Raff and Kaufman (1983) note that protein and morphological phylogenies are not always congruent using the prime example of chimpanzees and man being morphologically distinct but with protein

sequences greater than 99% identical. Any correspondence of phylogentic trees is probably the result of long term averaging of morphological and molecular rates while noncorrespondence can result from variation in rates in evolution. Disregarding fortuitous events, complete congruence of protein and morphological data sets may support a recent, rapid range expansion; so rapid that populations have not had time to become different. Partial congruence of data sets may be indicative of differing selective pressures on the populations as would be expected of a well established species. Noncongruence would be indicative of differential evolutionary rates among character sets and is probably the norm.

Although morphological and molecular evolution appear independent, a strong correlation between karyotypic and morphological evolution was hypothesized by Bush *et al.*, (1977) such that chromosome evolution may be responsible for the genomic rearrangements important in morphological evolution. Contrary to this, Gold (1980) found chromosomal evolution to be slower in the rapidly speciating fish genus *Notropis* while Baker and Bickham (1980) found that bats are morphologically conservative but enjoy disparate rates of chromosome change.

To better understand the evolutionary implications of these questions concerning *Sceloporus*, comprehensive studies of other species of the genus are necessary. To at least provide a comparable base for answering the evolutionary questions and implications of Sites' work with *S. grammicus*, it is desirable to select an organism

which is similar to *S. grammicus*. *Sceloporus olivaceus*, a member of the *spinosus* species group, exhibits several similarities to *S. grammicus* and appears to represent a highly appropriate organismal model. The two species are comparable in their arboreal life styles, adaptability to a wide variety of habitats, and large Ne (Kerster, 1964). Additionally, chromosomal evolution of the *spinosus* group may have proceeded in a manner similar to *S. grammicus*. Cole (1970) analyzed the karyotypes of the *spinosus* group and has shown that the species group has undergone considerable chromosomal evolution (primarily involving centric fusions) relative to the proposed ancestral iguanid karyotype (2n=36; Gorman, 1973). Cole concludes that speciation within the group probably involved faunal restrictions and derivation by geographic isolation of *spinosus* prototype populations.

S. olivaceus is a large lizard which is adapted to semiarid subtropical thorn forests, live oak woodlands, subtropical thorn scrub with riparian woodland, and desert-grassland habitats (Cole, 1970). Its range is bounded in Texas to the north by the Red River and to the east by a line approximating longitude 96°W. The western boundary follows the Cap Rock escarpment and the western edge of the Edwards and Stockton Plateaus. In Texas, *S. olivaceus* inhabits the Tamaulipan biome to the south, the Gulf Coastal Plain, the Blackland Prairies, Cross Timbers, Edwards and Stockton Plateaus, portions of the Red River Rolling Plains, and Gypsum Plains east of the Cap Rock escarpment and is absent from the Eastern Timbers and Llano Estacado. In Mexico, the species ranges south to southern

Tamaulipas inhabiting the Tamaulipan biome and is limited to the west by the Sierra Madre Oriental northward to Coahuila. Peripheral populations occur in valleys along the eastern edge of the Sierra Madre Oriental, some encompassing portions of the Chihuahuan desert. The limiting characteristic throughout the range of *S. olivaceus* appears to be the presence or absence of trees.

Smith (1939) placed *S. olivaceus* in the *spinosus* group, one of the largest and most diverse of the genus. The *spinosus* group has recieved much systematic attention and at least five different phylogenies have been proposed (Smith, 1939; Cole, 1970; Bussjaeger, 1971; Hall, 1973; Larsen and Tanner, 1975). The placement of *S. olivaceus* with its relatives are but one point of contention within the phylogenies. Smith (1939) places *S. olivaceus* near *S. spinosus* diverging from *S. horridus* while Cole (1970) notes *S. horridus* diverged from *S. olivaceus*. Bussjaeger (1971) depicts *S. cautus* (*undulatus* group) as being derived from *S. olivaceus* with *S. olivaceus* branching from some *spinosus*-like stock. He further notes the *undulatus* group probably arose from either *S. cautus* or *S. olivaceus*. Hall (1973) groups 10 species together including *S. olivaceus*, *S. cautus*, *S. spinosus*, *S. undulatus*, and *S. horridus* among others, all derived from some *magister*-like stock. Hall further notes that the *formosus* group is derived from this lineage as well, while Smith (1939) depicts the *formosus* group as the primitive form of the genus. Larsen and Tanner (1975) note that *S. cautus* recently speciated from *S. olivaceus* and place *S. cautus* in the *spinosus* group. The *S. cautus*-*S. olivaceus* relationship is compounded further by Hall (*in* Bussjaeger, 1971) who believes *S.*

cautus is another population of *S. olivaceus*. Hall says that *S. cautus* and *S. olivaceus* intergrade south and west of Monterrey such that there may be a circle of subspecies whose terminal populations are fully sympatric. Additionally, Smith (1939) noted that *S. cautus* may be the missing link between the *undulatus* and *spinosus* groups as *S. cautus* appears to have been derived from *S. spinosus*.

A detailed in-depth study of *S. olivaceus* and its supposed relatives is required to better understand their evolutionary relationships. This study proposes to examine morphological, chromosomal, and electrophoretic variation in *S. olivaceus* to answer questions concerning its evolution and to provide a base for future studies concerning its relatives.

The objectives of this study are:

1) To assess chromosomal variation in *S. olivaceus*. The species is generally considered karyotypically monomorphic (2n=22) however Cole (1970) identified individuals heterozygous for a pericentric inversion. Analysis of individuals throughout the range may identify other chromosomal polymorphisms.

2) To assess morphological variation in *S. olivaceus*. The species is presently monotypic and analysis of geographic variation may reveal population/habitat relationships. Further, phenotypic analysis may reveal a correlation to any discovered chromosomal polymorphisms.

3) To document allozyme variation in *S. olivaceus*. Genic analysis of the species may reveal patterns of concordance with any chromosomal polymorphisms, morphological characters, or habitat.

Further, genic analysis would provide information concerning population structure such as levels of gene flow, past bottlenecks, or founder events. Additionally, genic analysis of the supposed closely related species to *S. olivaceus* (*S. cautus* and *S. spinosus* with *S. cyanogenys* as an outgroup) may reveal a phylogenetic relationship. A recent study by Ferguson (1982) relegates *S. cautus* to the *spinosus* group based on close morphological affinities to *S. olivaceus* and electrophoretic analysis may support these findings.

It is quite obvious that the genus *Sceloporus* has enjoyed a complex evolutionary history. The results of this study should augment Sites' (1980) findings and add to the growing body of knowledge concerning the evolution of the sceloporines.

MATERIALS AND METHODS

A total of 438 live *S. olivaceus* were collected throughout its range in Texas and Mexico. Individuals were hand collected or noosed utilizing 12' collapsible fishing poles tipped with 15 lb. plastic coated leader material. Each individual was numbered on the belly with indelible ink for identification and maintained in moistened bags in a styrofoam cooler for the duration of each field trip. Specimens were then processed in the laboratory and tagged for deposit in the Texas Cooperative Wildlife Collection (TCWC). Figure 1 and Table 1 indicate the collection localities and sample designations used in this study.

Standard karyotypes for 270 *S. olivaceus* were obtained from bone marrow using the method of Patton (1967) as modified by Lee (1969) and Cole and Leavens (1971) for lizards and Baker *et al.* (1982). Lizards were stressed with .10-.20 cc yeast/sugar/water solution injected intramuscularly and incubated for 24 hours in a cage on a slide warmer set at 50 C. The lizards were sacrificed, both femurs removed and macerated to liberate the marrow. The marrow was treated with about 0.50 ml 0.075M KCl hypotonic solution and one drop of 0.05% colchicine for 40 minutes at room temperature, then centrifuged at moderate speed for about one minute. After most of the supernatant was pippetted off, the remaining button was fixed and gently aspirated in Carnoy's solution (3 parts methanol:1 part acetic acid) and centrifuged for about one minute; this fixation procedure was applied two additional times. Following the final fix, two to three drops of the cell suspension were dropped from a height of

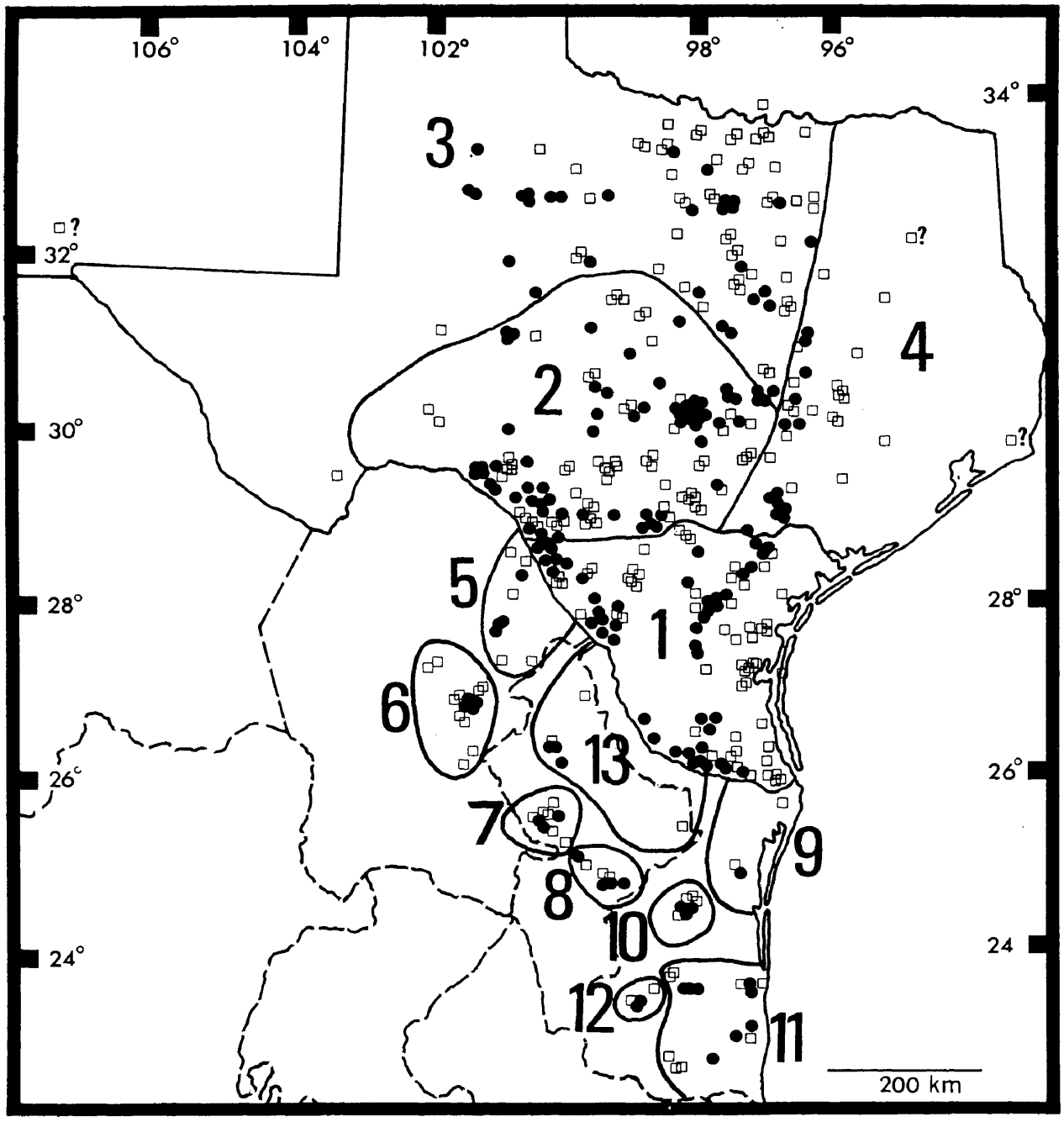


Figure 1. Collecting and sampling localities for Sceloporus olivaceus used in this study. Dark circles represent specimens analyzed karyotypically and electrophoretically; open squares represent borrowed specimens.

Table 1. Sample designations for Sceloporus olivaceus utilized in this study. Boundaries generally follow county lines or geographic area (see Figure 1).

Sample	Locality
1	Texas: South Texas
2	Texas: Edwards Plateau
3	Texas: North Texas
4	Texas: East Texas
5	Mexico: Nuevo Rosita area, Coahuila
6	Mexico: Monclova area, Coahuila
7	Mexico: Huasteca Canyon area, Nuevo Leon
8	Mexico: Linares and Santa Rosa Canyon area, Nuevo Leon
9	Mexico: Northeastern Tamaulipas
10	Mexico: San Carlos area, Tamaulipas
11	Mexico: Southern Tamaulipas
12	Mexico: Juamave Valley, Tamaulipas
13	Mexico: Northern Nuevo Leon

about one foot onto clean microscope slides; the slides were flame dried and stained in a 2% solution of Giemsa in 0.01M phosphate buffer for five minutes. Mitotic metaphases were scored using a Leitz microscope.

Allozyme variation was analyzed in 409 *S. olivaceus*, 30 *S. cautus*, nine *S. spinosus*, and 17 *S. cyanogenys* utilizing horizontal starch gel electrophoresis and staining techniques as described by Selander *et al.* (1971) and modified by Webster *et al.* (1972), McKinney *et al.* (1972), Spohn and Guttman (1976) and Sites and Greenbaum (1983). Heart, liver, lung, and leg muscles were removed from sacrificed animals, labeled, and stored in NUNC tubes in liquid nitrogen and then in the laboratory freezer at -70 C. Liver and heart, muscle, and lung tissues were separately homogenized in an equal volume of grinding solution (0.1M Tris, 0.001M EDTA, $5X10^{-5}$ M NADP, pH 7.0) and centrifuged at 4 C for 20 minutes. The aqueous extract was collected and stored in NUNC tubes at -70 C. Gel types and stains followed Sites and Greenbaum (1983) (Table 2). The data were analyzed using the BIOSYS-1 (Swofford and Selander, 1981) computer program. The input data were encoded by the genotype of each locus/individual/sample. BIOSYS-1 computed the following statistics: allele frequencies for all loci/sample; proportion of polymorphic loci per sample (P); average number of heterozygous loci per individual per sample (H); mean number of alleles/locus/sample (A); Rogers' (1972) genetic similarity (S); Nei's (1972) genetic distance (D); UPGMA clusters of Nei's (1978) unbiased genetic identity, Nei's (1978) unbiased genetic distance, Nei's (1978) unbiased minimum

Table 2. Gel buffers, voltage, time of run, and stains utilized during this study. Buffers are from Selander et al. (1971).

Gel Buffer	Voltage	Time of Run (Hrs.)	Stains
Tris-Citrate 8.0	100-110 v	8-10	Malate dehydrogenase (MDH-1 and -2) Isocitrate dehydrogenase (IDH) Lactate dehydrogenase (LDH-1 and -2) Malic enzyme (ME) Glutamic oxylate transaminase (GOT-1 and -2)
	75 ma	8	Phosphoglucomutase (PGM-1 and -2) Indophenol oxidase (IPO)
Discontinuous Tris-Hydrochloric Acid	200 v	4	-Glycerophosphate dehydrogenase (-GPD) Esterase (EST-1 and -4) Xanthine dehydrogenase (XDH) Leucine aminopeptidase (LAP) Albumin (ALB) General protein (GP-1 and -2)
Tris-Maleic EDTA Dilute (2:1)	200 v	4	Alcohol dehydrogenase (ADH)

distance, Nei's (1972) minimum distance, Rogers' (1972) genetic distance, modified Rogers distance (Wright, 1978), Nei's (1972) genetic identity, Nei's (1972) genetic distance; Wright's (1978) F-statistics; and the distance Wagner procedure (Farris, 1972).

Morphological variation was analyzed in 969 *S. olivaceus* using several multistate, meristic, and morphometric characters. Each individual was sexed and sorted into one of two classes. Blair (1960) noted male *S. olivaceus* became sexually active at a snout-vent length (SVL) of about 65 mm while females became sexually active at an SVL of about 80 mm. For this study, the juvenile age class (1) included males with SVL<65 mm and females with SVL<80 mm; the adult age class (2) included males with SVL≥65 mm and females with SVL≥80 mm. Morphometric characters were measured with dial calipers to the nearest 0.01 mm and standardized in various combinations of ratios for statistical treatment.

Patterns of head squamation representing multistate characters were determined for:

Prefrontal Scales - in medial contact=1 or separate=2

Frontal Scales - entire=1*, in medial contact=1 or split=2*

Frontoparietal Scales - in medial contact=1 or separate=2

Preliminary evaluation of a small sample of specimens revealed some mutilation due to method of collection or improper curation. Based on this analysis, left and/or right side meristic characters were scored where appropriate. The meristic characters were analyzed as follows:

DORSALS - the number of scales in a longitudinal row from the posterior margin of the interparietal scale to the base of the tail (above anal plate).

SAB - the number of scales around the body midway between the limbs.

FEMPOR - the number of femoral pores on both thighs.

INTFEM - the number of scales between the most medial femoral pores.

AURLBLL(R) - the number of enlarged auricular lobules on the anterior opening of the left (right) ear opening.

PSTROSTL - the number of postrostral scales bordering the rostral.

CANTHL(R) - the number of canthal scales along the left (right) canthal ridge.

SCBINTP - the number of scales bordering the interparietal scale.

INTPSTAN - the number of scales between the enlarged postanal scales in males.

CRCMORBL(R) - the number of circumorbital scales separating the enlarged left (right) side supraoculars from medial head scales.

SPOCLL(R) - the number of the medial-most left (right) row of supraoculars.

SPLBLL(R) - the number of left (right) side supralabials.

INFRLBLL(R) - the number of left (right) side infralabials.

SBLBLL(R) - the number of left (right) side sublabials.

SCBTSBL - the number of chin scales between the third pair of sublabials.

PSTMNTL - the number of left side postmental scales, excluding infralabials.

TOELAML(R) - the number of 4th toe lamallae on the left (right) hindfoot.

The morphometric characters taken include:

SVL - the snout-vent length taken from the tip of the snout to the anterior margin of the vent.

SOL - the snout-occiput length taken from the tip of the snout to the posterior margin of the interparietal scale.

SERL - the snout-ear length measured from the tip of the snout to the upper anterior margin of the ear.

SEL - the snout-eye length measured from the tip of the snout to the anterior edge of the bony orbit.

EYERL - the eye-ear length measured from the posterior edge of the bony orbit to the anterior edge of the ear.

ED - the eye diameter measured from the anterior to the posterior edge of the bony orbit.

IL - the interparietal length measured from the front to the back edge of the interparietal scale.

IW - the interparietal width taken across the posterior edge of the interparietal scale.

SW - the snout width measured at the nostrils.

HW - the head width measured just anterior to the ear openings.

FL - the femur length measured from the body to the flexed knee.

TBL - the tibia length measured from the flexed knee to the heel.

HL - the humerus length measured from the body to the flexed elbow.

FML - the forearm length measured from the flexed elbow to the wrist joint.

The following ratios were used: R1=SOL/SVL; R2=SERL/SVL; R3=SEL/SVL; R4=EYERL/SERL; R5=ED/SERL; R6=SW/HW; R7=IL/SOL; R8=IW/HW; R9=FL/SVL; R10=TBL/SVL; R11=HL/SVL; R13=HW/SVL.

The Amdahl 470 V/6 computer at the Texas A&M University Data Processing Center was used to analyze univariate and multivariate statistics. The Analysis of Variance (ANOVA) procedure with the Duncan option, Student's t-test, frequency procedure and means procedure, available in the Statistical Analysis System (SAS, Institute Inc., 1979) were used to test univariate statistics. Interpopulational relationships considering all characters simultaneously were tested using the multivariate analysis of variance (MANOVA) of SAS-79 in conjunction with a canonical analysis. The Numerical Taxonomy System (NT-SYS) (Rohlf and Kishpaugh, 1972) was used to cluster all samples by phenetic similarity. The sample (OTU) means for all morphometric and meristic characters generated matrices of Pearson's product-moment correlation coefficients and intersample phenetic distance coefficients. The unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal, 1973) produced phenograms generated on both the correlation and

distance coefficients.

Morphological analyses were performed on specimens field collected or borrowed from museums and private collections. The following list of acronyms identifies museums and collections utilized during this study.

AMNH American Museum of Natural History, New York, New York (Dr. Richard G. Zweifel).

CAS California Academy of Sciences, San Francisco, California (Jens V. Vindum)

KU Museum of Natural History, Kansas University, Lawrence, Kansas (Dr. William E. Duellman)

MSUM Michigan State University, East Lansing, Michigan (Leslie P. Fay)

MWSU Midwestern State University, Wichita Falls, Texas (Dr. W. W. Dalquest)

SDNHM San Diego Museum of Natural History, San Diego, California (Jim Berrian)

SHSU Sam Houston State University, Huntsville, Texas (Dr. Ralph R. Moldenhauer)

SU Baylor University Museum, Waco, Texas (Dr. David Lintz)

TAI Texas A&I University, Kingsville, Texas (Dr. Allan H. Chaney)

TCWC Texas Cooperative Wildlife Collection, Texas A&M University, College Station, Texas

(Dr. James R. Dixon)

REO R. Earl Olson, Museum Services Associates, Grandy, Minnesota

RESULTS

Chromosomal Analysis

Cole (1970) described four general karyotypes for the nine species of the *spinosus* group. *S. olivaceus* is a member of the *lundelli*-type (2n=22) which is composed of six pairs of macrochromosomes and five pairs of smaller elements. Of the macrochromosomes, the 1st, 3rd, 4th, and 5th largest are metacentric while the 2nd and 6th largest are submetacentric. Pair number 2 possesses a terminal secondary constriction. The five pairs of smaller elements include four metacentrics and one subtelocentric or submetacentric pair. Figure 2 depicts a typical karyotype of *S. olivaceus*.

Several atypical karyotypes in *S. olivaceus* were reported by Cole (1970). These involved two individuals (one male from Val Verde County, Texas and one female from Travis County, Texas) heterozygous for a pericentric inversion in pair number 7. The same atypical male also exhibited an abberant cell consisting of a loop in one macrochromosome of pair number 1 resulting from a sister chromatid fusion. Of the 270 specimens karyotyped throughout its range, all karyotypes appeared to be normal as depicted in Figure 2.

Figure 2. Karyotype of Sceloporus olivaceus (male, TCWC 60966).

Morphological Variation

Non-Geographic Variation

Age variation within a sex was assessed in contiguous counties (Texas: Uvalde, Medina, Bexar, Bandara, Comal, Edwards) of sample 2 to provide an adequate sample size. Head scale character state frequencies among age classes by sex are depicted in Table 3. Both sexes exhibit approximately the same prefrontal scale condition in their respective age classes. Juveniles of both sexes exhibit prefrontals in contact (46%) and prefrontals separate (54%). A slight ontogenetic shift occurs in the adult age class with males exhibiting prefrontals in contact (57%) and prefrontals separate (43%) while females exhibit 54% prefrontals in contact and 46% prefrontals separate. The frontal and frontoparietal head scale conditions show no ontogenetic shifts in either sex. The frontals in contact and frontoparietals separate predominate in both sexes and age groups.

Means for all characters among age classes for males and females were compared to test ontogenetic variation in meristic characters and ratios. Statistical procedures involved the use of Analysis of Variance with the Duncan option of the Statistical Analysis System (SAS, Institute Inc., 1979) to determine significant character variation between age classes of each sex.

The results for males (Table 4) indicate that there were no significant differences between the age classes for the meristic characters. Ratios R1, R5, R6, R7, and R8 were significantly

Table 3. Character state frequencies among age classes in a sample of Sceloporus olivaceus from Central Texas. Numbers represent actual proportion of individuals for each character state; parentheses enclose percentages for each group. Age class 1=juvenile; age class 2=adult. Character state 1=contact, 1*=entire, 2=separate, 2*=split.

Age Class by Sex	Prefrontal		Frontal			Frontoparietal	
	1	2	1*	1	2*	1	2
Males							
1 n=28	13 (.46)	15 (.54)	-	19 (.68)	9 (.32)	2 (.07)	26 (.93)
2 n=49	28 (.57)	21 (.43)	2 (.04)	35 (.71)	12 (.25)	4 (.08)	45 (.92)
Females							
1 n=28	13 (.46)	15 (.54)	-	24 (.86)	4 (.14)	4 (.14)	24 (.86)
2 n=50	27 (.54)	23 (.46)	-	39 (.78)	11 (.22)	7 (.14)	43 (.86)

Table 4. Age variation in meristic and ratio characters in male Sceloporus olivaceus from a sample in Central Texas. Vertical lines connect characters that are not significantly different. Age class 1=juvenile, age class 2=adult.

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
DORSALS	1	29	30.52(1.15)	28.00	33.00	0.21	3.78
	2	49	30.47(0.98)	28.00	32.00	0.14	3.22
SAB	1	28	34.61(2.20)	30.00	39.00	0.42	6.36
	2	48	34.96(1.58)	31.00	38.00	0.23	4.53
FEMPOR	1	27	26.70(2.15)	23.00	32.00	0.41	8.03
	2	49	27.57(2.22)	23.00	32.00	0.32	8.04
INTFEM	1	27	8.04(0.94)	6.00	10.00	0.18	11.69
	2	49	7.76(1.20)	5.00	10.00	0.17	15.47
AURLBLL	1	28	3.11(0.79)	2.00	4.00	0.15	25.30
	2	48	2.81(0.76)	2.00	4.00	0.11	27.10
AURLBLR	1	27	3.11(0.80)	2.00	5.00	0.15	25.73
	2	49	2.78(0.71)	2.00	4.00	0.10	25.76
PSTROSTL	1	29	3.55(0.69)	2.00	5.00	0.13	19.31
	2	47	3.53(0.83)	2.00	5.00	0.12	23.50
CANTHL	1	29	2.00(0.27)	1.00	3.00	0.05	13.36
	2	49	1.96(0.20)	1.00	2.00	0.03	10.20
CANTHR	1	29	2.00(0.27)	1.00	3.00	0.05	13.36
	2	48	1.96(0.20)	1.00	2.00	0.03	10.31

Table 4. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
SCBINTP	1	28	6.00(0.94)	4.00	7.00	0.18	15.71
	2	47	6.15(0.83)	4.00	8.00	0.12	13.56
INTPSTAN	1	28	2.07(0.72)	0.00	3.00	0.14	34.58
	2	48	2.08(0.74)	1.00	3.00	0.13	36.46
CRCMORBL	1	29	8.34(0.97)	7.00	10.00	0.18	11.67
	2	48	8.35(0.86)	7.00	10.00	0.12	10.33
CRCMORBR	1	28	8.32(0.86)	7.00	10.00	0.16	10.37
	2	47	8.30(1.10)	5.00	10.00	0.16	13.28
SPOCLL	1	29	5.28(0.59)	5.00	7.00	0.11	11.21
	2	49	5.29(0.50)	5.00	7.00	0.07	9.46
SPOCLR	1	29	5.28(0.59)	5.00	7.00	0.11	11.21
	2	49	5.33(0.52)	5.00	7.00	0.07	9.69
SPLBLL	1	29	5.14(0.35)	5.00	6.00	0.07	6.83
	2	46	5.13(0.34)	5.00	6.00	0.05	6.64
SPLBLR	1	29	5.17(0.38)	5.00	6.00	0.07	7.43
	2	47	5.09(0.35)	4.00	6.00	0.05	6.90
INFRLBLL	1	29	6.76(0.44)	6.00	7.00	0.08	6.44
	2	46	6.74(0.49)	6.00	8.00	0.07	7.29

Table 4. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
INFRLBLR	1	29	6.90(0.49)	6.00	8.00	0.09	7.09
	2	47	6.87(0.54)	6.00	8.00	0.08	7.80
SBLBLL	1	28	3.75(0.44)	3.00	4.00	0.08	11.76
	2	49	3.78(0.47)	3.00	5.00	0.07	12.41
SBLBLR	1	28	3.68(0.48)	3.00	4.00	0.09	12.93
	2	49	3.78(0.47)	3.00	5.00	0.07	12.41
PSTMNTL	1	29	3.72(0.59)	3.00	5.00	0.11	15.88
	2	49	3.71(0.65)	2.00	5.00	0.09	17.38
TOELAML	1	29	20.97(1.66)	15.00	24.00	0.31	7.91
	2	48	21.42(1.49)	19.00	24.00	0.21	6.93
TOELAMR	1	28	21.11(1.37)	18.00	24.00	0.26	6.49
	2	48	21.54(1.52)	18.00	24.00	0.22	7.03
SCBTSBL	1	27	13.11(1.42)	11.00	16.00	0.27	10.86
	2	48	12.58(1.41)	10.00	15.00	0.20	11.22
R1	1	26	0.23(0.02)	0.21	0.31	0.00	10.08
	2	47	0.21(0.01)	0.20	0.22	0.00	3.07
R2	1	28	0.24(0.02)	0.22	0.29	0.00	6.98
	2	48	0.23(0.01)	0.19	0.25	0.00	4.35

Table 4 . (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
R3	1	28	0.09(0.01)	0.08	0.10	0.00	7.90
	2	48	0.08(0.01)	0.07	0.10	0.00	6.23
R4	1	27	0.37(0.04)	0.30	0.45	0.01	11.50
	2	47	0.37(0.04)	0.29	0.49	0.01	11.10
R5	1	27	0.46(0.03)	0.41	0.53	0.01	6.01
	2	47	0.45(0.03)	0.38	0.53	0.00	6.52
R6	1	28	0.22(0.02)	0.17	0.25	0.00	8.97
	2	49	0.20(0.02)	0.15	0.24	0.00	9.24
R7	1	27	0.28(0.04)	0.22	0.40	0.01	13.75
	2	47	0.26(0.02)	0.22	0.31	0.00	7.24
R8	1	26	0.32(0.08)	0.24	0.57	0.01	23.31
	2	47	0.24(0.03)	0.19	0.31	0.00	12.13
R9	1	27	0.20(0.02)	0.16	0.23	0.00	8.15
	2	46	0.21(0.01)	0.17	0.23	0.00	6.76
R10	1	28	0.20(0.03)	0.16	0.29	0.01	15.85
	2	49	0.20(0.03)	0.17	0.28	0.00	12.70
R11	1	28	0.14(0.02)	0.10	0.22	0.00	14.51
	2	49	0.14(0.01)	0.12	0.18	0.00	8.68

Table 4. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
R12	1	28	0.14(0.02)	0.11	0.22	0.00	14.39
	2	49	0.14(0.01)	0.11	0.17	0.00	7.86
R13	1	28	0.21(0.02)	0.18	0.25	0.00	7.56
	2	49	0.20(0.01)	0.16	0.23	0.00	6.22

different ($P<0.05$) indicating ontogenetic change in head measurements.

Females (Table 5) demonstrate significant differences ($P<0.05$) in FEMPOR, AURLBLL, and TOELAMR. All ratios except R9, R10, R11, and R12 were significantly different ($P<0.05$) indicating ontogenetic change in all but limb/SVL ratios.

Significant age differences among the sexes is apparent from the ratio analysis while the meristic data indicate little differences. Differences between female age classes for FEMPOR are probably the result of resolution errors. Differences between female age classes for AURLBLL are probably due to judgemental errors. In analyzing geographic variation, only adults (males, SVL≥65 and females, SVL≥ 80) were used to minimize age variation influences.

Sexual variation was analyzed in three subsamples of locality 2 in which adequate numbers of specimens were available. The first subsample consisted of contiguous counties (Texas: Uvalde, Medina, Bexar, Bandera, Comal, Edwards) with a sample size of 99. As large sample sizes may differentiate characters significantly, a smaller second subsample (Texas: Bexar County) with a sample size of 56 was used. A third subsample (Texas: Kinney, Val Verde Counties) consisting of a sample size of 37 was also used. The Student's t-test was utilized to determine differences between the sexes. Table 6 summarizes the results of subsample 1, Table 7 subsample 2, and Table 8 subsample 3.

The sexes from subsample 1 differed significantly in DORSALS, SAB, and INTFEM ($P<0.01$) and SPOCLL, SPOCLR, INFRLBLL, and INFRLBLR

Table 5. Age variation in meristic and ratio characters in female Sceloporus olivaceus from a sample in Central Texas. Verticle lines connect characters that are not significantly different. Age class 1=juvenile, age class 2=adult.

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
DORSALS	1	29	30.66(1.20)	29.00	33.00	0.22	3.93
	2	50	31.12(1.08)	29.00	33.00	0.15	3.47
SAB	1	27	35.41(2.14)	31.00	41.00	0.41	6.03
	2	48	36.10(1.94)	31.00	41.00	0.28	5.37
FEMPOR	1	28	25.96(1.93)	21.00	29.00	0.37	7.45
	2	49	27.00(2.25)	22.00	32.00	0.32	8.32
INTFEM	1	26	8.42(1.21)	5.00	11.00	0.24	14.31
	2	50	8.60(0.93)	7.00	11.00	0.13	10.77
AURLBLL	1	30	3.17(0.75)	2.00	5.00	0.14	23.58
	2	50	2.78(0.76)	2.00	5.00	0.11	27.47
AURLBLR	1	29	3.10(0.86)	2.00	5.00	0.16	27.70
	2	50	2.80(0.81)	2.00	5.00	0.11	28.86
PSTROSTL	1	27	3.78(0.58)	2.00	4.00	0.11	15.28
	2	46	3.65(0.67)	2.00	4.00	0.10	18.45
CANTHL	1	30	2.00(0.26)	1.00	3.00	0.05	13.13
	2	50	1.92(0.27)	1.00	2.00	0.04	14.27
CANTHR	1	30	1.97(0.18)	1.00	2.00	0.03	9.28
	2	50	1.92(0.27)	1.00	2.00	0.04	14.27

Table 5. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
SCBINTP	1	28	6.04(1.04)	4.00	8.00	0.20	17.16
	2	50	6.30(0.95)	4.00	8.00	0.13	15.13
CRCMORBL	1	28	8.18(1.12)	6.00	11.00	0.21	13.74
	2	50	8.46(0.81)	6.00	10.00	0.12	9.61
CRCMORBR	1	27	8.19(0.92)	7.00	10.00	0.18	11.26
	2	50	8.50(0.74)	7.00	10.00	0.10	8.65
SPOCLL	1	29	5.45(0.63)	5.00	7.00	0.12	11.59
	2	50	5.60(0.61)	5.00	7.00	0.09	10.82
SPOCLR	1	28	5.50(0.64)	5.00	7.00	0.12	11.61
	2	50	5.58(0.64)	5.00	7.00	0.09	11.50
SPLBLL	1	28	5.18(0.39)	5.00	6.00	0.07	7.53
	2	49	5.18(0.44)	5.00	7.00	0.06	8.51
SPLBLR	1	29	5.07(0.26)	5.00	6.00	0.05	5.09
	2	50	5.20(0.40)	5.00	6.00	0.06	7.77
INFRLBLL	1	29	6.93(0.53)	6.00	8.00	0.10	7.65
	2	50	6.98(0.43)	6.00	8.00	0.06	6.13
INFRLBLR	1	29	7.10(0.49)	6.00	8.00	0.09	6.80
	2	50	7.14(0.50)	6.00	8.00	0.07	6.94

Table 5. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
SBLBLL	1	30	3.90(0.48)	3.00	5.00	0.09	12.32
	2	50	3.90(0.42)	3.00	5.00	0.06	10.68
SBLBLR	1	30	3.83(0.38)	3.00	4.00	0.07	9.89
	2	50	3.90(0.30)	3.00	4.00	0.07	7.77
PSTMNTL	1	30	3.80(0.71)	2.00	5.00	0.13	18.80
	2	50	3.86(0.73)	2.00	5.00	0.10	18.88
TOELAML	1	30	21.90(1.65)	19.00	25.00	0.30	7.52
	2	48	21.54(1.47)	19.00	25.00	0.21	6.84
TOELAMR	1	30	21.90(1.35)	19.00	24.00	0.25	6.16
	2	47	21.09(1.59)	18.00	25.00	0.23	7.52
SCBTSBL	1	30	12.87(1.48)	10.00	16.00	0.27	11.50
	2	49	13.10(1.43)	10.00	16.00	0.20	10.93
R1	1	28	0.22(0.02)	0.19	0.30	0.00	9.22
	2	50	0.20(0.01)	0.18	0.22	0.00	4.25
R2	1	30	0.24(0.02)	0.21	0.30	0.00	6.34
	2	50	0.22(0.01)	0.20	0.24	0.00	4.24
R3	1	29	0.09(0.01)	0.07	0.11	0.00	8.89
	2	50	0.08(0.01)	0.07	0.09	0.00	6.61

Table 5 . (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
R4	1	29	0.38(0.04)	0.30	0.48	0.01	11.59
	2	49	0.37(0.04)	0.30	0.49	0.01	10.55
R5	1	29	0.46(0.03)	0.40	0.56	0.01	7.34
	2	50	0.43(0.02)	0.39	0.46	0.00	4.04
R6	1	29	0.21(0.02)	0.16	0.27	0.00	11.47
	2	49	0.19(0.01)	0.15	0.21	0.00	7.76
R7	1	28	0.28(0.03)	0.24	0.39	0.01	10.96
	2	50	0.25(0.02)	0.21	0.29	0.00	7.38
R8	1	28	0.31(0.07)	0.22	0.56	0.01	21.87
	2	49	0.23(0.03)	0.16	0.34	0.00	12.67
R9	1	28	0.20(0.02)	0.16	0.23	0.00	8.54
	2	47	0.20(0.01)	0.17	0.23	0.00	7.26
R10	1	30	0.20(0.03)	0.17	0.27	0.01	13.96
	2	50	0.19(0.03)	0.16	0.28	0.00	13.51
R11	1	30	0.14(0.01)	0.13	0.16	0.00	4.83
	2	50	0.14(0.01)	0.12	0.12	0.00	7.27
R12	1	30	0.14(0.01)	0.12	0.16	0.00	6.87
	2	50	0.14(0.01)	0.12	0.18	0.00	8.99

Table 5. (Continued).

Characters	Age Class	N	$\bar{X}$(SD)	Min	Max	SE	CV
R13	1	30	0.21(0.02)	0.18	0.24	0.00	8.30
	2	49	0.19(0.01)	0.16	0.21	0.00	6.97

Table 6. Sexual variation in adult Sceloporus olivaceus from subsample 1. Significant t-values are indicated by *(P 0.05) or **(P 0.01).

Character	Males N	Males $\bar{X}$(SD)	Males Range	Females N	Females $\bar{X}$(SD)	Females Range	t
DORSALS	49	30.47(0.98)	28-32	50	31.12(1.08)	29-33	-3.137**
SAB	48	34.96(1.58)	31-38	48	36.10(1.94)	31-41	-3.172**
FEMPOR	49	27.57(2.22)	23-32	49	27.00(2.25)	22-32	1.268
INTFEM	49	7.76(1.20)	5-10	50	8.60(0.93)	7-11	-3.918**
AURLBLL	48	2.81(0.76)	2-4	50	2.78(0.76)	2-5	0.211
AURLBLR	49	2.76(0.71)	2-4	50	2.80(0.81)	2-5	-0.160
PSTROSTL	47	3.53(0.83)	2-5	46	3.65(0.67)	2-4	-0.768
CANTHL	49	1.96(0.20)	1-2	50	1.92(0.27)	1-2	0.814
CANTHR	48	1.96(0.20)	1-2	50	1.92(0.27)	1-2	0.791
SCBINTP	47	6.15(0.83)	4-8	50	6.30(0.95)	4-8	-0.832
CRCMORBL	48	8.35(0.86)	7-10	50	8.46(0.81)	6-10	0.732
CRCMORBR	47	8.30(1.10)	5-10	50	8.50(0.74)	7-10	0.865
SPOCLL	49	5.29(0.50)	5-7	50	5.60(0.61)	5-7	-2.035*
SPOCLR	49	5.33(0.52)	5-7	50	5.58(0.64)	5-7	-2.356*
SPLBLL	47	5.13(0.34)	5-6	49	5.18(0.44)	5-7	-0.424
SPLBLR	47	5.09(0.35)	4-6	50	5.20(0.40)	5-6	-1.498
INFRLBLL	46	6.74(0.49)	6-8	50	6.98(0.43)	6-8	-2.551*
INFRLBLR	47	6.87(0.54)	6-8	50	7.14(0.50)	6-8	-2.549*
SBLBLL	49	3.78(0.47)	3-5	50	3.90(0.42)	3-5	-1.434
SBLBLR	49	3.78(0.47)	3-5	50	3.90(0.30)	3-4	-1.567
PSTMNTL	49	3.71(0.65)	2-5	50	3.86(0.73)	2-5	-1.054
TOELAML	48	21.42(1.49)	19-24	48	21.54(1.47)	19-25	0.556
TOELAMR	48	21.54(1.52)	18-24	47	21.09(1.59)	18-25	1.500
SCBTSBL	48	12.58(1.41)	10-15	49	13.10(1.43)	10-16	-1.796

Table 6. (Continued).

Character	Males N	Males $\bar{X}$(SD)	Males Range	Females N	Females $\bar{X}$(SD)	Females Range	t
R1	47	0.21(0.01)	.20-.22	50	0.20(0.01)	.18-.21	2.718**
R2	48	0.23(0.01)	.19-.25	50	0.22(0.01)	.20-.24	1.503
R3	48	0.08(0.01)	.07-.10	50	0.08(0.01)	.07-.09	1.272
R4	47	0.37(0.04)	.29-.49	49	0.37(0.04)	.30-.49	-0.674
R5	47	0.45(0.03)	.38-.53	50	0.43(0.02)	.40-.46	1.408
R6	49	0.20(0.02)	.15-.24	49	0.19(0.01)	.15-.21	0.727
R7	47	0.26(0.02)	.22-.31	50	0.25(0.02)	.21-.29	1.261
R8	47	0.24(0.03)	.19-.31	49	0.23(0.03)	.16-.34	0.739
R9	46	0.21(0.01)	.17-.23	47	0.20(0.01)	.17-.23	1.142
R10	49	0.20(0.03)	.17-.28	50	0.19(0.03)	.16-.28	1.165
R11	49	0.14(0.01)	.12-.18	50	0.14(0.01)	.12-.17	0.691
R12	49	0.14(0.01)	.11-.17	50	0.14(0.01)	.12-.18	-0.155
R13	49	0.20(0.01)	.16-.23	49	0.19(0.01)	.16-.21	1.884

Table 7. Sexual variation in adult Sceloporus olivaceus from subsample 2. Significant t-values are indicated by *(P 0.05) or **(P 0.01).

Character	Males N	Males $\bar{X}$(SD)	Males Range	Females N	Females $\bar{X}$(SD)	Females Range	t
DORSALS	27	30.55(0.93)	28-32	29	31.21(1.15)	29-33	-2.339*
SAB	26	34.38(1.68)	31-38	29	36.07(1.79)	33-40	-3.603**
FEMPOR	27	27.67(2.18)	23-32	29	27.31(2.30)	22-32	0.595
INTFEM	27	7.81(1.08)	6-10	29	8.52(0.95)	7-11	-2.584*
AURLBLL	27	2.48(0.64)	2-4	29	2.48(0.57)	2-4	-0.008
AURLBLR	27	2.52(0.64)	2-4	29	2.34(0.61)	2-4	1.033
PSTROSTL	25	3.68(0.63)	2-4	25	3.72(0.61)	2-4	-0.228
CANTHL	27	1.93(0.27)	1-2	29	1.86(0.35)	1-2	0.770
CANTHR	26	1.92(0.27)	1-2	29	1.86(0.35)	1-2	0.725
SCBINTP	26	6.42(0.70)	5-8	29	6.38(0.98)	5-8	0.192
CRCMORBL	26	8.46(0.86)	7-10	29	8.38(0.90)	6-10	0.346
CRCMORBR	25	8.44(1.12)	6-10	29	8.55(0.69)	7-10	-0.433
SPOCLL	27	5.37(0.56)	5-7	29	5.48(0.57)	5-7	-0.738
SPOCLR	27	5.41(0.57)	5-7	29	5.52(0.63)	5-7	-0.681
SPLBLL	24	5.08(0.28)	5-6	28	5.07(0.26)	5-6	0.157
SPLBLR	25	5.16(0.37)	5-6	29	5.24(0.44)	5-6	-0.739
INFRLBLL	24	6.63(0.49)	6-7	29	6.97(0.33)	6-8	-2.894**
INFRLBLR	25	6.76(0.52)	6-8	29	7.17(0.54)	6-8	-2.849**
SBLBLL	27	3.74(0.53)	3-5	29	3.93(0.26)	3-4	-1.700
SBLBLR	27	3.66(0.48)	3-4	29	3.93(0.26)	3-4	-2.539*
PSTMNTL	27	3.89(0.58)	3-5	29	3.93(0.59)	3-5	-0.269
TOELAML	26	21.50(1.48)	19-24	27	21.56(1.63)	19-25	-0.130
TOELAMR	27	21.56(1.28)	19-23	28	21.04(1.45)	18-24	1.409
SCBTSBL	26	12.81(1.33)	10-15	28	12.79(1.42)	10-15	0.059

Table 7. (Continued).

Character	Males			Females			t
	N	$\bar{X}$(SD)	Range	N	$\bar{X}$(SD)	Range	
R1	26	0.21(0.01)	.20-.22	29	0.21(0.01)	.18-.22	4.238**
R2	27	0.23(0.01)	.22-.25	29	0.23(0.01)	.21-.24	3.003**
R3	27	0.08(0.01)	.08-.10	29	0.08(0.01)	.07-.09	2.436*
R4	26	0.35(0.03)	.29-.43	28	0.35(0.02)	.30-.40	0.546
R5	26	0.45(0.02)	.41-.51	29	0.44(0.01)	.40-.46	2.614*
R6	27	0.20(0.01)	.17-.23	28	0.19(0.01)	.15-.21	2.077*
R7	26	0.26(0.02)	.22-.31	29	0.25(0.02)	.21-.29	2.869**
R8	26	0.25(0.03)	.20-.31	28	0.24(0.03)	.17-.34	1.967
R9	27	0.20(0.01)	.17-.22	29	0.20(0.02)	.17-.23	1.526
R10	27	0.19(0.01)	.17-.21	29	0.19(0.01)	.17-.21	1.473
R11	27	0.14(0.01)	.12-.16	29	0.14(0.01)	.12-.16	0.505
R12	27	0.14(0.01)	.11-.15	29	0.14(0.01)	.12-.15	-0.152
R13	27	0.20(0.01)	.16-.23	28	0.19(0.02)	.16-.21	2.042*

Table 8 . Sexual variation in adult Sceloporus olivaceus from subsample 3. Significant t-values are indicated by *(P 0.05) or **(P 0.01).

Character	Males			Females			t
	N	$\bar{X}$(SD)	Range	N	$\bar{X}$(SD)	Range	
DORSALS	19	30.84(1.38)	28-33	18	31.22(1.17)	29-33	-0.905
SAB	19	35.16(1.68)	32-38	17	35.71(1.61)	32-38	-1.000
FEMPOR	19	26.47(2.29)	22-30	18	26.89(2.11)	24-31	-0.573
INTFEM	19	8.16(1.21)	6-11	18	8.72(0.96)	7-11	-1.574
AURLBLL	19	3.00(0.75)	2-4	18	2.83(0.79)	2-4	0.661
AURLBLR	19	2.95(0.91)	2-5	18	2.94(0.73)	2-4	0.011
PSTROSTL	19	3.68(0.67)	2-4	18	3.67(0.69)	2-4	0.079
CANTHL	19	2.00(-)	-	18	2.00(-)	-	-
CANTHR	19	2.00(-)	-	18	2.00(-)	-	-
SCBINTP	19	6.26(0.93)	5-8	18	6.00(1.08)	4-8	0.789
CRCMORBL	18	8.44(0.86)	7-9	18	8.17(1.04)	6-10	0.874
CRCMORBR	18	8.17(0.71)	7-9	18	8.28(0.75)	7-10	-0.457
SPOCLL	18	5.17(0.38)	5-6	18	5.33(0.49)	5-6	-1.144
SPOCLR	18	5.22(0.43)	5-6	18	5.17(0.38)	5-6	0.410
SPLBLL	19	5.16(0.37)	5-6	18	5.06(0.24)	5-6	1.000
SPLBLR	19	5.11(0.32)	5-6	18	5.17(0.38)	5-6	-0.530
INFRLBLL	19	6.58(0.61)	5-7	18	6.72(0.57)	6-8	-0.738
INFRLBLR	19	6.74(0.56)	6-8	18	7.00(0.59)	6-8	-1.383
SBLBLL	19	3.74(0.56)	3-5	18	3.61(0.50)	3-4	0.719
SBLBLR	19	3.53(0.51)	3-4	18	3.67(0.59)	3-5	-0.767
PSTMNTL	19	3.79(0.54)	3-5	18	4.17(0.62)	3-5	-1.980
TOELAML	19	21.68(1.33)	19-24	16	22.68(1.08)	21-25	-2.459*
TOELAMR	19	21.68(1.83)	19-24	17	22.76(0.97)	21-24	-2.248*
SCBTSBL	19	13.27(1.50)	11-16	18	13.56(1.34)	11-16	-0.175

Table 8. (Continued).

Character	Males N	Males $\bar{X}$(SD)	Males Range	Females N	Females $\bar{X}$(SD)	Females Range	t
R1	19	0.20(0.01)	.19-.22	18	0.19(0.01)	.18-.20	3.983**
R2	19	0.22(0.01)	.21-.24	18	0.22(0.01)	.21-.23	2.446*
R3	19	0.08(0.01)	.08-.09	18	0.08(0.01)	.07-.09	2.093*
R4	19	0.36(0.02)	.33-.43	18	0.37(0.03)	.33-.45	-0.937
R5	19	0.45(0.02)	.41-.50	18	0.44(0.02)	.40-.48	1.940
R6	19	0.21(0.02)	.17-.24	18	0.19(0.02)	.15-.23	3.546**
R7	19	0.27(0.02)	.23-.31	18	0.26(0.01)	.23-.28	2.178*
R8	19	0.26(0.03)	.19-.34	18	0.21(0.02)	.18-.23	6.062**
R9	14	0.20(0.01)	.17-.27	13	0.21(0.01)	.19-.23	-0.944
R10	19	0.18(0.01)	.17-.20	18	0.19(0.01)	.17-.21	-2.669*
R11	19	0.14(0.01)	.11-.15	18	0.15(0.01)	.13-.17	-2.607*
R12	19	0.14(0.01)	.10-.16	18	0.14(0.01)	.12-.17	-1.565
R13	19	0.19(0.01)	.17-.22	18	0.20(0.01)	.18-.21	-0.656

($P<0.05$) while R1 was the only ratio showing significant sexual variation ($P<0.01$). Females exhibited higher counts in those differing meristic characters while males tended to have greater snout-occiput length.

The sexes from subsample 2 differed significantly in SAB, INFRLBLL, and INFRLBLR ($P<0.01$) and DORSALS, INTFEM, and SBLBLR ($P<0.05$) while ratios R1, R2, and R7 ($P<0.01$) and R3, R5, R6 and R13 ($P<0.05$) showed significant sexual variation. Females exhibited higher counts in those differing meristic characters while males tended to have greater snout-occiput length, snout-ear length, snout-eye length, eye diameter, snout width, interparietal length, and head width.

The sexes from subsample 3 differed significantly in TOELAML and TOELAMR ($P<0.05$) while ratios R1, R6, and R8 ($P<0.01$) and R2, R3, R7, R10, and R11 showed significant sexual variation ($P<0.05$). Females exhibited higher counts in toe lamellae and greater tibia and humerus lengths while males tended to exhibit greater snout-occiput length, snout-ear length, snout-eye length, snout width, interparietal length, and interparietal width.

Because significant sexual differences occurred in the three subsamples, the sexes were separated for further analysis. This was done to minimize the effects of sexual dimorphism and to permit duplicate data sets for further analyses.

Geographic Variation: Univariate Analysis

Head scale character state frequencies between sexes for the 13 sample localities are depicted in Table 9. Inadequate numbers or mutilation of specimens caused low sample sizes such that trends among sample localities are tenuous. Males tended to have contacting prefrontals (57%-100%) over all samples except locality 13 in which prefrontals were separate in 56% of the specimens. Females tended to have contacting prefrontals in seven localities (52%-100%), equal percentages of contacting to separate prefrontals in two localities, and three localities with separate prefrontals predominating (54%-100%). Both sexes exhibited a predominance of contacting frontal scales (67%-100%) in all localities. Both sexes exhibited separate frontoparietals (60%-100%) in all localities except localitiy 7 with females exhibiting equal percentages of contacting to separate frontoparietals. The data indicate no particular trends tying head scale character state to a specific geographic region.

The means procedure and ANOVA-Duncan option provided basic statistics for assessing geographic variation for each sex in the 13 sample localities. FEMPOR, INTFEM, and TOELAML showed significant differences ($P<0.05$) over all localities in both sexes. In males, PSTMNTL, SCBINTP, SPOCLL, SCBTSBL, and in females CRCMORBL, INFRLBLL, SBLBLL showed significant differences ($P<0.05$) over all localities. These variable characters appeared to be random with respect to habitat or geographic feature.

The ratio data appear to support the meristic data in that 10 of the 13 ratios showed nonsignificant variation while R1, R4, and R6

Table 9. Character state frequencies between sexes among 13 samples of adult Sceloporus olivaceus. Numbers represent actual proportion of individuals for each character state; parentheses enclose percentages for each state. Character state 1=contact, 1*=entire, 2=separate, 2*=split.

Sample	Sex	Prefrontal		Frontal			Frontoparietal	
		1	2	1*	1	2*	1	2
1	M	40(.57)	30(.43)	-	56(.79)	15(.21)	5(.07)	66(.93)
	F	31(.50)	31(.50)	1(.02)	44(.71)	17(.27)	7(.11)	56(.89)
2	M	69(.61)	44(.39)	3(.03)	84(.74)	26(.23)	14(.12)	100(.88)
	F	75(.56)	58(.44)	-	94(.71)	39(.29)	19(.14)	114(.86)
3	M	41(.71)	17(.29)	1(.02)	58(.98)	-	8(.14)	51(.86)
	F	36(.46)	42(.54)	1(.01)	65(.83)	12(.16)	8(.10)	70(.90)
4	M	19(.82)	4(.18)	1(.04)	18(.78)	4(.18)	3(.13)	20(.87)
	F	11(.52)	10(.48)	-	18(.86)	3(.14)	3(.14)	18(.86)
5	M	6(.67)	3(.37)	-	6(.67)	3(.33)	4(.44)	5(.56)
	F	1(.25)	3(.75)	-	3(.75)	1(.25)	-	4(1.0)
6	M	11(.73)	4(.27)	-	14(.88)	2(.12)	3(.19)	13(.82)
	F	3(1.0)	-	-	2(.67)	1(.33)	1(.33)	2(.67)
7	M	6(.86)	1(.14)	-	5(.71)	2(.29)	-	7(1.0)
	F	1(.50)	1(.50)	-	2(1.0)	-	1(.50)	1(.50)
8	M	1(1.0)	-	-	1(1.0)	-	-	1(1.0)
	F	2(1.0)	-	-	2(1.0)	-	-	2(1.0)
9	M	3(.60)	2(.40)	-	5(1.0)	-	2(.40)	3(.60)
	F	-	1(1.0)	-	1(1.0)	-	-	1(1.0)
10	M	11(1.0)	-	-	10(.91)	1(.09)	3(.27)	8(.73)
	F	4(.67)	2(.33)	-	5(.83)	1(.17)	1(.17)	5(.83)
11	M	16(.89)	2(.11)	-	17(.94)	1(.06)	3(.17)	15(.83)
	F	9(.82)	2(.18)	-	10(.91)	1(.09)	-	11(.10)
12	M	3(1.0)	-	-	3(1.0)	-	-	3(1.0)
	F	-	-	-	-	-	-	-
13	M	4(.44)	5(.56)	-	6(.67)	3(.33)	1(.11)	8(.89)
	F	3(.75)	1(.25)	-	4(1.0)	-	-	4(1.0)

seemed to exhibit random variation over all sample localities. The ratio data provided no information in establishing any habitat or geographic related trends.

Figures 3 and 4 illustrate variation in adult male and adult female DORSALS, respectively. Locality 12 for males (Figure 3) is based on a low sample size of three individuals and exhibits a high DORSAL mean. There are no definite geographic trends in the DORSAL counts of the sexes throughout the 13 sample localities. This is further exemplified in the SAB counts (Figures 5 and 6) for adult males and females, respectively.

Figures 7 and 8 illustrate adult male and female FEMPOR counts, respectively. This character as indicated above showed significant differences in both sexes. No distinct geographical trends are apparent and the variability appears to be random.

Geographic Variation: Multivariate Analysis

Several herpetological studies have subjected multiple characters to statistical analysis to better interpret populational relationships (Fritts, 1974; Iverson, 1977; Jackson, 1973; Larsen and Tanner, 1974; Sites, 1982; Sites and Dixon, 1982). Meristic and morphometric data for adults of each sex of *S. olivaceus* were statistically analyzed by the MANOVA-Canonical discriminant function. The hypothesis of no overall interlocality differences was tested by Hotelling-Lawley's Trace, Pillai's Trace, Wilk's lambda, and Roy's Maximum Root Criterion, each with a significant F value ($P<0.0001$). It is assumed that the samples are not all part of the same

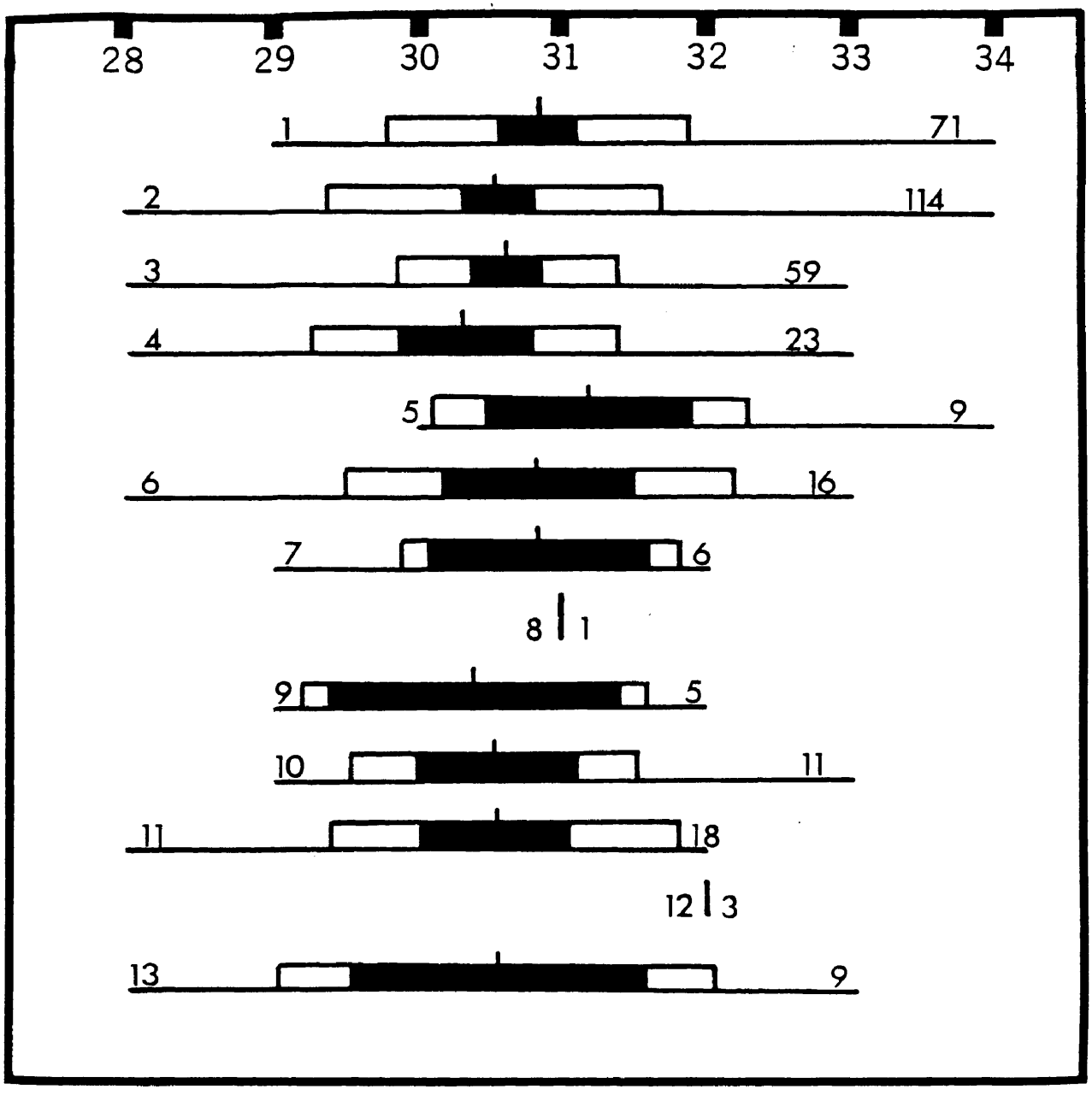


Figure 3. Dice-Leraas diagram of DORSALS for adult male Sceloporus olivaceus from the 13 sample areas.

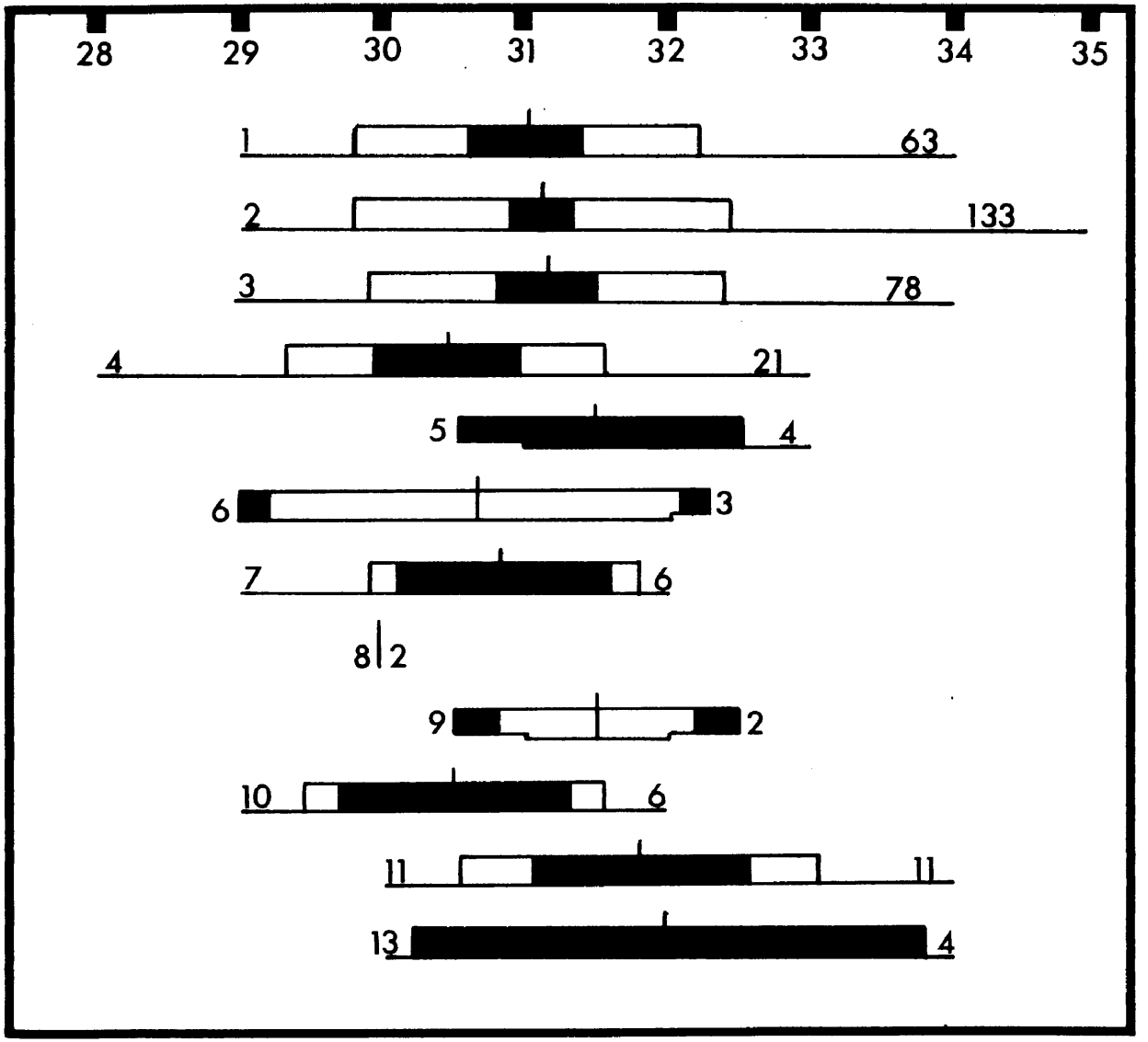


Figure 4. Dice-Leraas diagram of DORSALS for adult female Sceloporus olivaceus from the 13 sample areas.

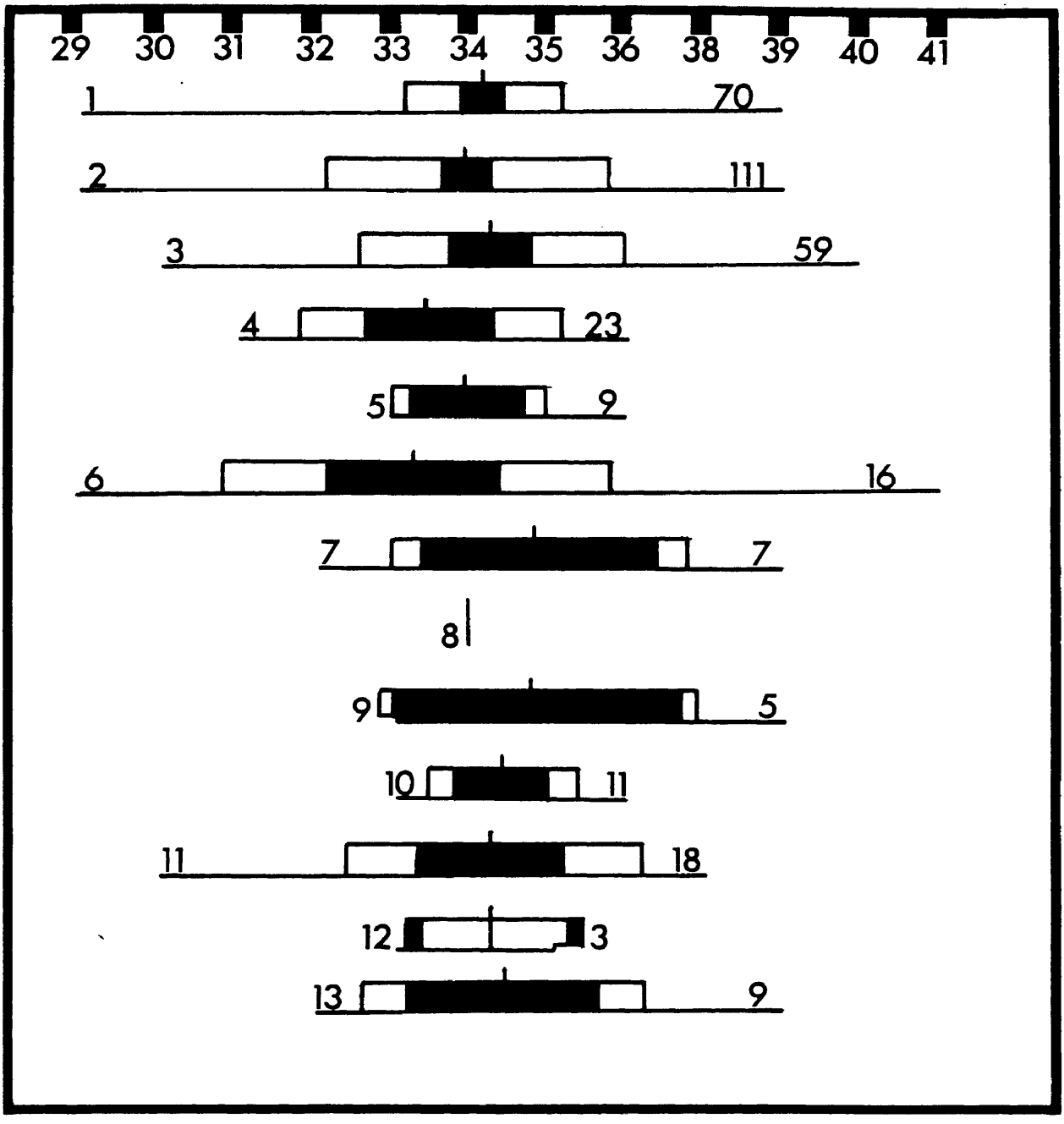


Figure 5. Dice-Leraas diagram for SAB for adult male Sceloporus olivaceus from the 13 sample areas.

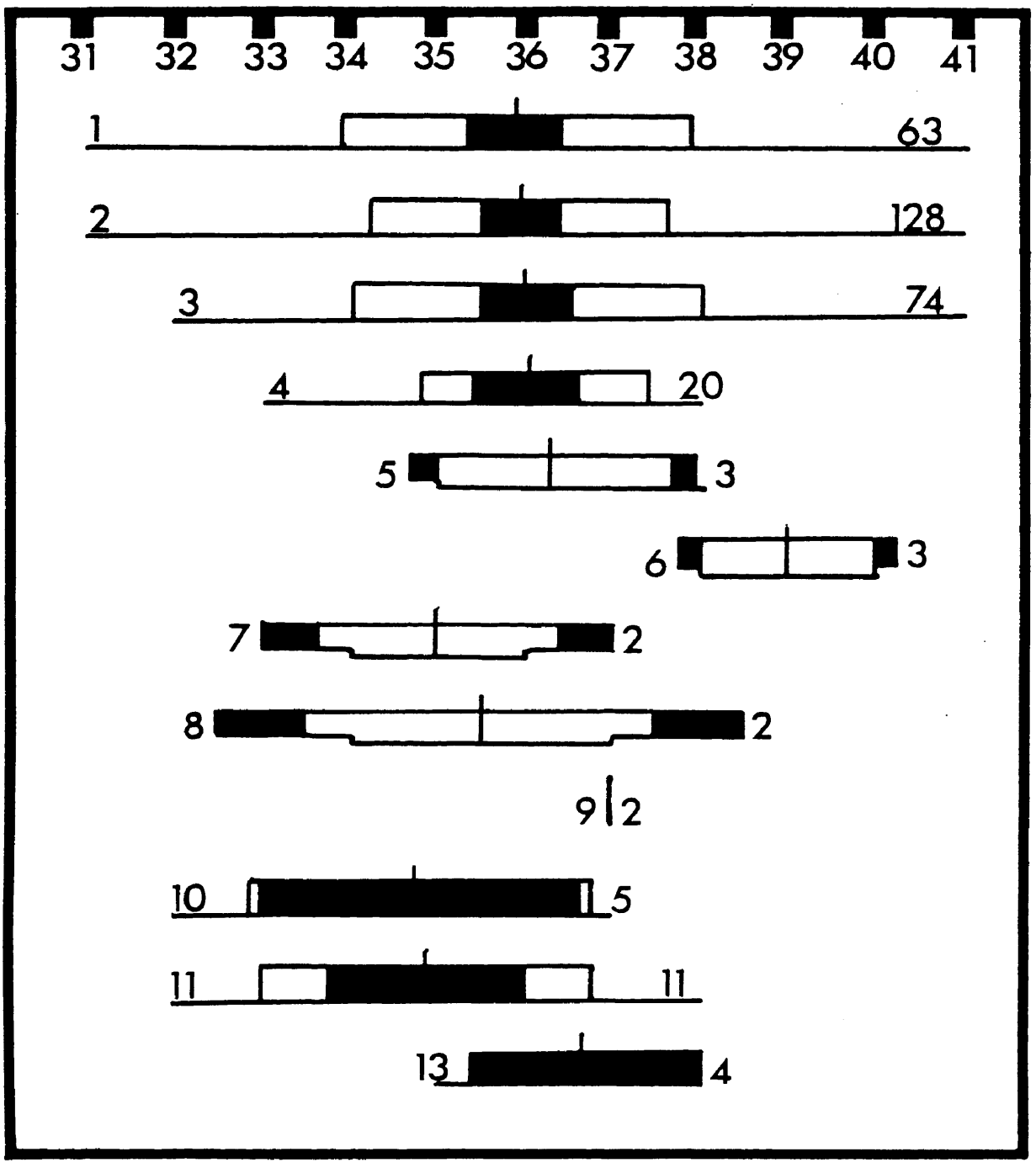
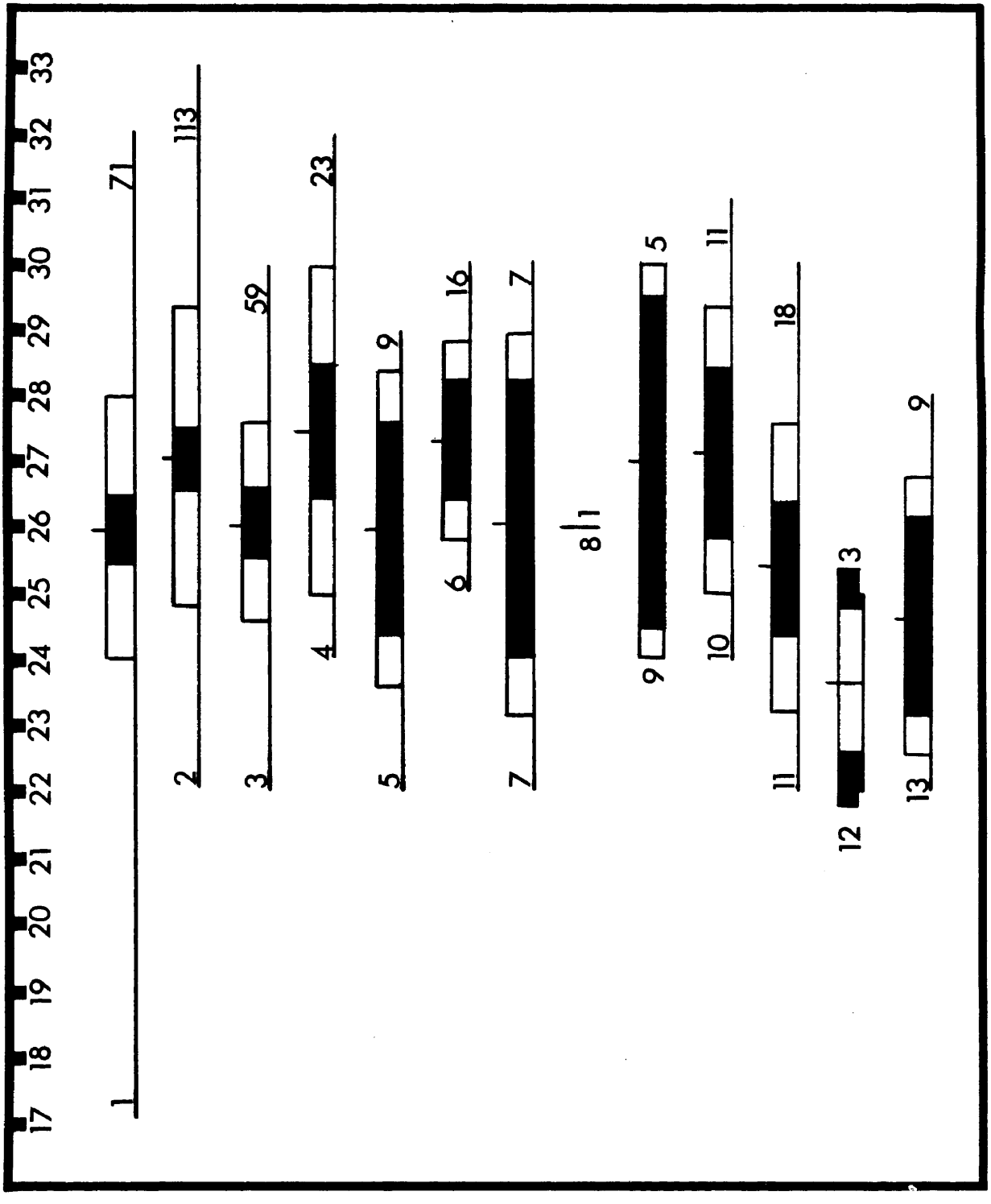


Figure 6. Dice-Leraas diagram for SAB for adult female Sceloporus olivaceus from the 13 sample areas.

Figure 7. Dice-Leraas diagram of FEMPORS for adult male Sceloporus olivaceus from the 13 sample areas.


17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33
1 71
2 113
3 59
4 23
5 9
6 16
7 7
8 1
9 5
10 11
11 18
12 3
13 9

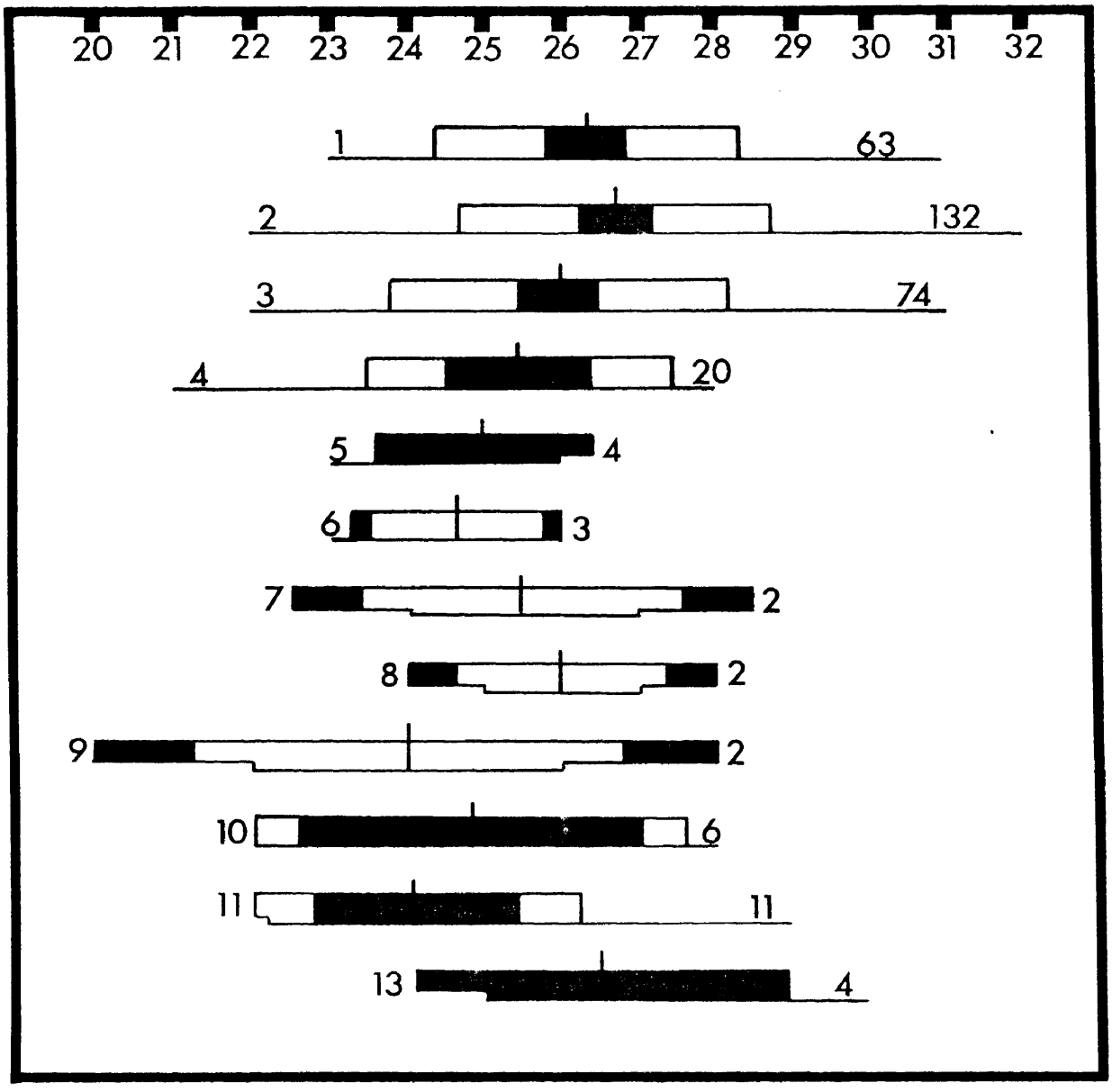


Figure 8. Dice-Leraas diagram of FEMPORS for adult female Sceloporus olivaceus from the 13 sample areas.

population. Sites (1982) notes that the chief assumption required by this test is that samples differ in some way for biological reasons and are not part of a homogeneous statistical universe.

Table 10 and Table 11 are summaries of the characteristic roots and percent of total variation for each canonical vector for the meristic data of males and females, respectively. For males, the first three vectors accounted for 68.29% of the total variation (Vector I - 37.67%, Vector II - 17.62%, Vector III - 13.00%). For females, the first three vectors accounted for 67.43% of the total variation (Vector I - 32.94%, Vector II - 22.97%, Vector III - 11.52%). The first two vectors were used to ordinate the multivariate means in a two-dimensional discriminant space depicting morphological relationships. The ellipses represent one standard deviation about the mean. Table 12 and Table 13 are the variable coefficients and percent influence of each variable on Vector I and Vector II for males and females, respectively.

In males (Figure 9), Vector I was most influenced by TOELAML (37.34%) and to a lesser extent by FEMPOR (9.14%). Vector I slightly discriminated samples 6, 12, and 13 along the axis but with major overlap by samples 5, 10, and 11. Vector II was most influenced by FEMPOR (19.85%) and SAB (14.37%). This axis discriminated sample 6 with the remaining samples showing no definite trend along the axis. A pattern appears to exist in that a north-south trend in sample centroids is evident from the upper left to lower right of Figure 9.

For females (Figure 10), Vector I was most influenced by TOELAML (16.29%), FEMPOR (13.08%), and DORSALS (12.78%). No distinct

Table 10. Characteristic root and percent of total variation attributed to each canonical vector in 13 samples of adult male Sceloporus olivaceus, meristic data.

Canonical Vector	Characteristic Root	Percent	Cumulative Percent
I	0.54159513	37.67	37.67
II	0.25339974	17.62	55.29
III	0.18698485	13.00	68.29
IV	0.13708493	9.53	77.82
V	0.10861163	7.55	85.37
VI	0.08139285	5.66	91.03
VII	0.04817652	3.35	94.38
VIII	0.03025767	2.10	96.48
IX	0.02566266	1.78	98.26
X	0.01228777	0.85	99.11
XI	0.00972661	0.68	99.79
XII	0.00268047	0.19	99.98

Table 11. Characteristic root and percent of total variation attributed to each canonical vector in 12 samples of adult female Sceloporus olivaceus, meristic data.

Canonical Vector	Characteristic Root	Percent	Cumulative Percent
I	0.37703977	32.94	32.94
II	0.26289725	22.97	55.91
III	0.13184919	11.52	67.43
IV	0.11012449	9.62	77.05
V	0.08483871	7.41	84.46
VI	0.06616555	5.78	90.24
VII	0.04445579	3.88	94.12
VIII	0.03163832	2.76	96.88
IX	0.01909791	1.67	98.55
X	0.01288468	1.13	99.68
XI	0.00347287	0.30	99.98

Table 12. Variable coefficients for canonical variates I and II and the percent influence of each variable on each vector for 13 samples of adult male Sceloporus olivaceus.

Character	Vector I		Vector II	
	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
DORSALS	.00385583	5.61	-.00547020	7.65
SAB	-.00378779	6.30	-.00897875	14.37
FEMPOR	-.00727019	9.14	.01642116	19.85
INTFEM	-.01017198	3.78	-.02295816	8.21
AURLBLL	-.00100251	0.14	-.01385340	1.85
PSTROSTL	.00041400	0.07	-.01824709	3.02
CANTHL	.03672418	3.45	-.03674630	3.32
SCBINTP	-.02098847	5.87	.00900081	2.42
CRCMORBL	.01375594	5.37	.00466889	1.76
SPOCLL	.00407012	1.04	-.02334386	5.68
SPLBLL	-.01006434	2.44	.0273948	6.37
INFRLBLL	-.00950725	3.06	-.02787905	8.60
SBLBLL	-.02264460	4.03	.01542182	2.64
PSTMNTL	.02594340	4.75	-.00944459	1.67
TOELAML	.0365018	37.48	.00859687	8.53
SCBTSBL	.01083970	6.63	-.00524831	3.08
INTPSTAN	-.00528264	0.84	.00909480	0.98

Table 13. Variable coefficients for canonical variates I and II and the percent influence of each variable on each vector for 12 samples of adult female Sceloporus olivaceus.

Character	Vector I		Vector II	
	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
DORSALS	.00985712	12.78	-.00632641	8.58
SAB	-.00624463	9.36	-.00263953	4.14
FEMPOR	-.01193947	13.08	.01976804	22.64
INTFEM	.02021247	7.20	.02054239	7.65
AURLBLL	.02383468	2.93	.00168464	0.22
PSTROSTL	.00986171	1.48	-.00614175	0.97
CANTHL	.00757290	0.61	-.01412898	1.20
SCBINTP	-.01129045	2.81	.02342797	6.09
CRCMORBL	.00838690	2.92	.03865180	14.07
SPOCLL	-.00810051	1.87	.00167712	0.41
SPLBLL	-.01019596	2.18	.05083604	11.39
INFRLBLL	-.04474796	12.91	-.00989507	2.99
SBLBLL	-.05828463	9.31	-.05818053	9.72
PSTMNTL	.02415749	3.93	.00677988	1.15
TOELAML	.01802012	16.29	-.00779095	7.35
SCBTSBL	-.00063538	0.34	-.00256417	1.43

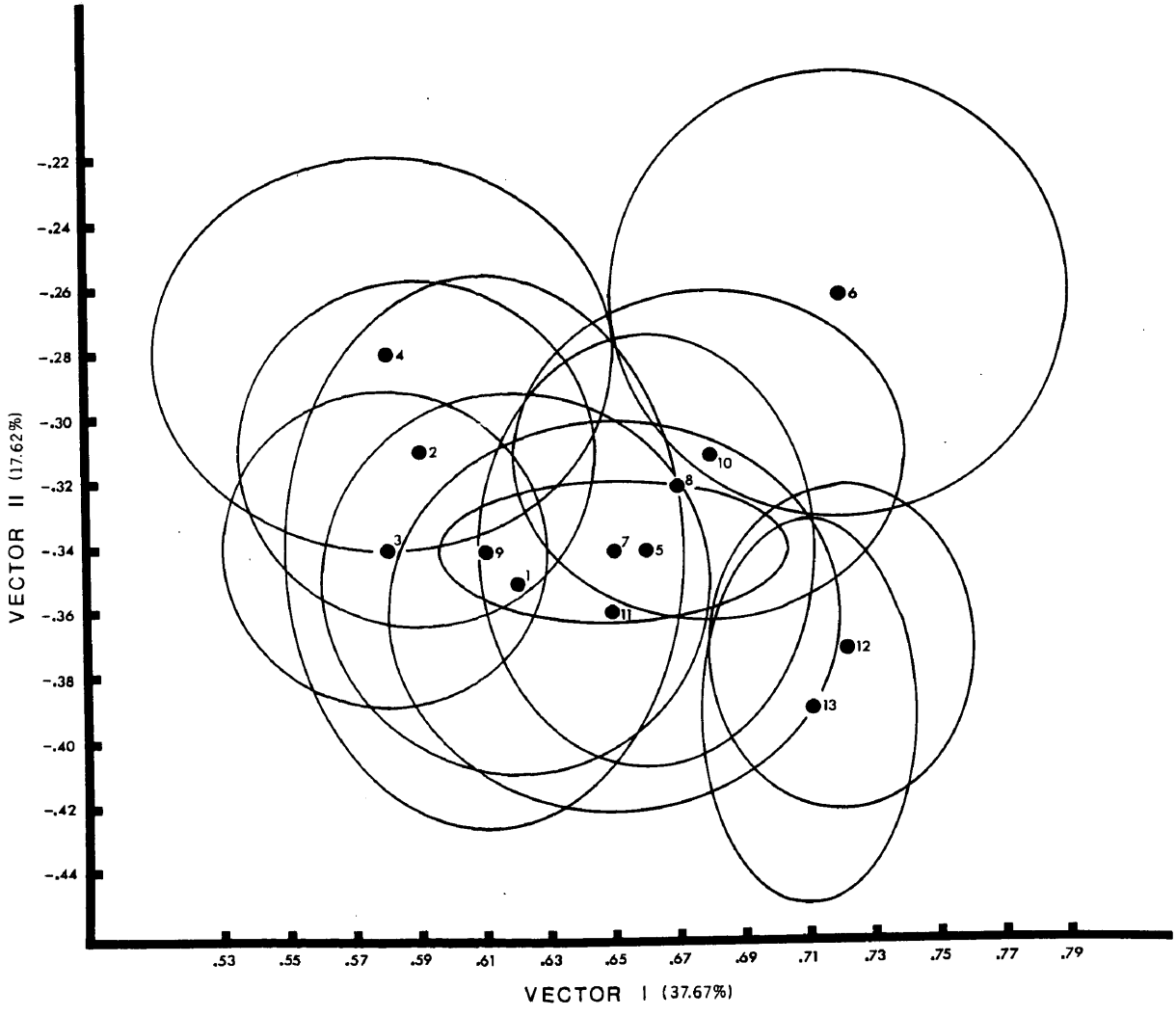


Figure 9. Projections on the first two canonical vectors of 13 samples of adult male Sceloporus olivaceus (meristic data).

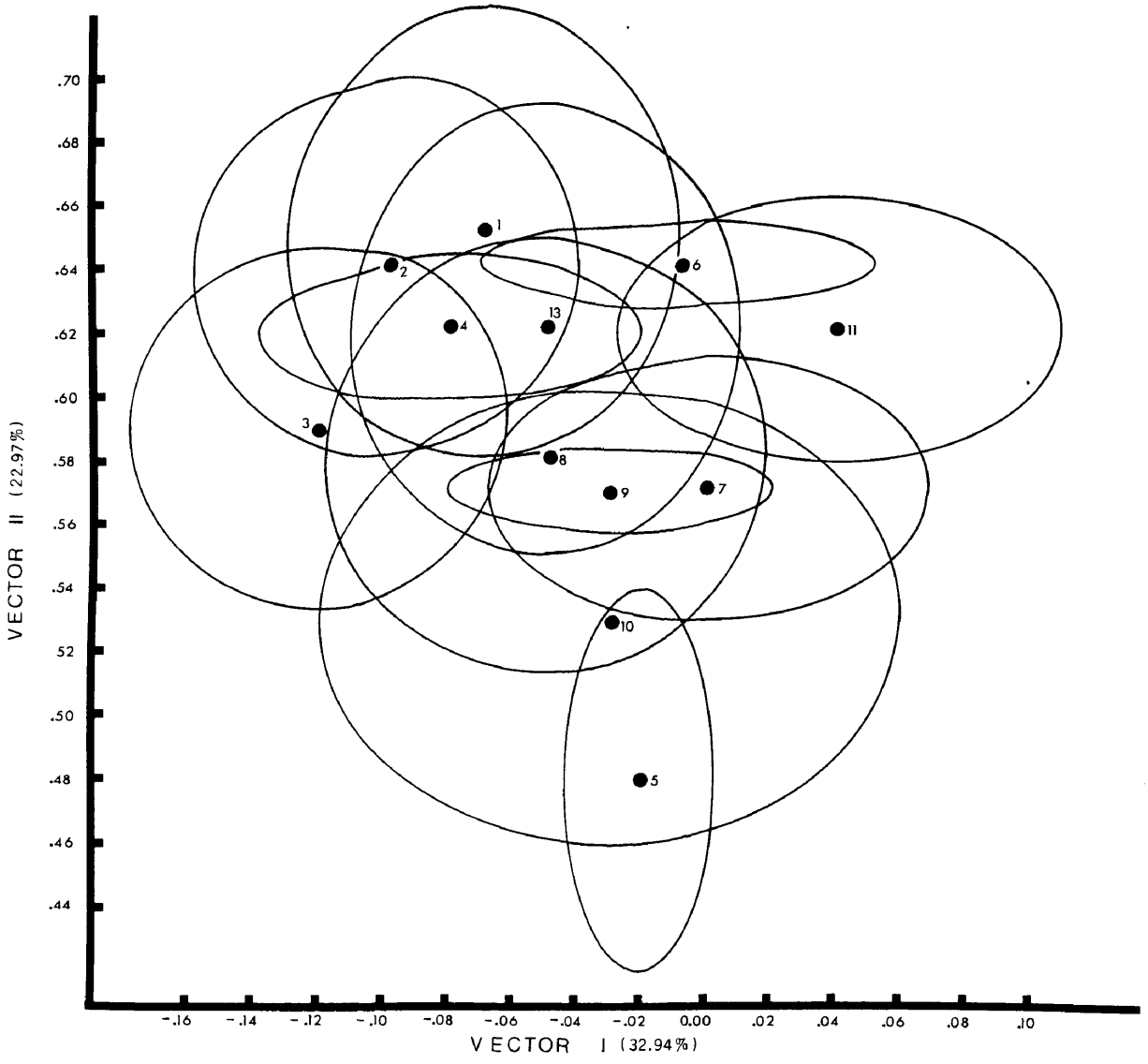


Figure 10. Projections on the first two canonical vectors of 12 samples of adult female Sceloporus olivaceus (meristic data).

dispersal pattern can be established along this axis. Vector II was most influenced by FEMPOR (27.64%), CRCMORBL (14.07%), and SPLBLL (11.39%). Sample 5 appears to be discriminated along this axis with sample 10 having major overlap with sample 10 and minor overlap with samples 7 and 8. A north-south trend is also apparent in sample centroids from left to right along Vector I.

As noted by Sites (1982), morphometric characters may contribute a significant amount of variation due to body size when using a multivariate analysis. This tendency can be ovecome by scaling for size or using ratios (Iverson, 1979a, 1979b). Characteristic roots for each canonical vector and the percent of total variation contributed by each for the ratio data is presented in Table 14 (males) and Table 15 (females).

In males, the first three vectors accounted for 66.53% of the total variation (Vector I - 28.99%, Vector II - 20.58%, Vector III - 16.96%). For females, the first three vectors accounted for 81.65% of the total variation (Vector I - 43.54%, Vector II - 23.63%, Vector III - 14.48%). Samples for both sexes were plotted onto a three-dimensional projection of the first three canonical vectors and the percent contribution of each ratio for each vector was calculated.

For males, ratio characters strongly influencing Vector I were R2 (20.74%), R1 (12.81%), and R6 (11.53%); for Vector II R6 (16.87%), R2 (16.49%), and R8 (15.10%); for Vector III, R13 (15.94%), R7 (15.63%), and R5 (10.80%) (see Table 16). Figure 11 depicts the male samples plotted in a three-dimensional space. Sample 4 and samples 5, 6, and 7 appear to be discriminated along Vector I. Vector II

Table 14. Characteristic root and percent of total variation attributed to each canonical vector in 13 samples of adult male Sceloporus olivaceus, ratio data.

Canonical Vector	Characteristic Root	Percent	Cumulative Percent
I	0.34602706	28.99	28.99
II	0.24567895	20.58	49.57
III	0.20241285	16.96	66.53
IV	0.16632001	13.93	80.46
V	0.07900133	6.62	87.08
VI	0.05559427	4.66	91.47
VII	0.04676175	3.92	95.66
VIII	0.03421266	2.87	98.53
IX	0.01229592	1.03	99.56
X	0.00506441	0.42	99.98
XI	0.00021709	0.02	100.00

Table 15. Characteristic root and percent of total variation attributed to each canonical vector in 12 samples of adult female Sceloporus olivaceus, ratio data.

Canonical Vector	Characteristic Root	Percent	Cumulative Percent
I	0.36837776	43.54	43.54
II	0.19992276	23.63	67.17
III	0.12248272	14.48	81.65
IV	0.05468388	6.46	88.11
V	0.04862861	5.75	93.86
VI	0.02381179	2.81	96.67
VII	0.01206657	1.43	98.10
VIII	0.00995363	1.18	99.28
IX	0.00487740	0.58	99.86
X	0.00128564	0.14	100.00

Table 16. Variable coefficients for canonical variates I, II, and III and the percent influence of each ratio on each vector for 13 samples of adult male Sceloporus olivaceus.

Ratio	Vector I		Vector II		Vector III	
	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
R1	-2.6647	12.81	1.2932	9.40	-2.4034	12.74
R2	3.7521	20.74	-1.9722	16.49	1.5806	9.63
R3	3.3343	6.41	-3.6224	10.54	-3.5305	7.48
R4	0.6080	5.55	0.4787	6.61	0.0241	0.24
R5	-0.7482	8.09	-0.0408	0.67	-0.9059	10.80
R6	-2.3995	11.53	-2.3124	16.81	1.5174	8.04
R7	-0.6371	3.98	-0.4955	4.68	-2.2680	15.63
R8	0.9200	5.31	1.7309	15.10	0.9236	5.87
R9	-1.3304	6.73	-0.1954	1.49	1.1705	6.51
R10	-2.0552	9.88	0.5793	4.22	-0.1240	0.66
R11	-0.8263	2.78	1.4975	7.62	-0.2468	0.92
R12	1.3367	4.50	-0.2773	1.42	1.4925	5.54
R13	0.3519	1.69	-0.6810	4.95	3.0061	15.94

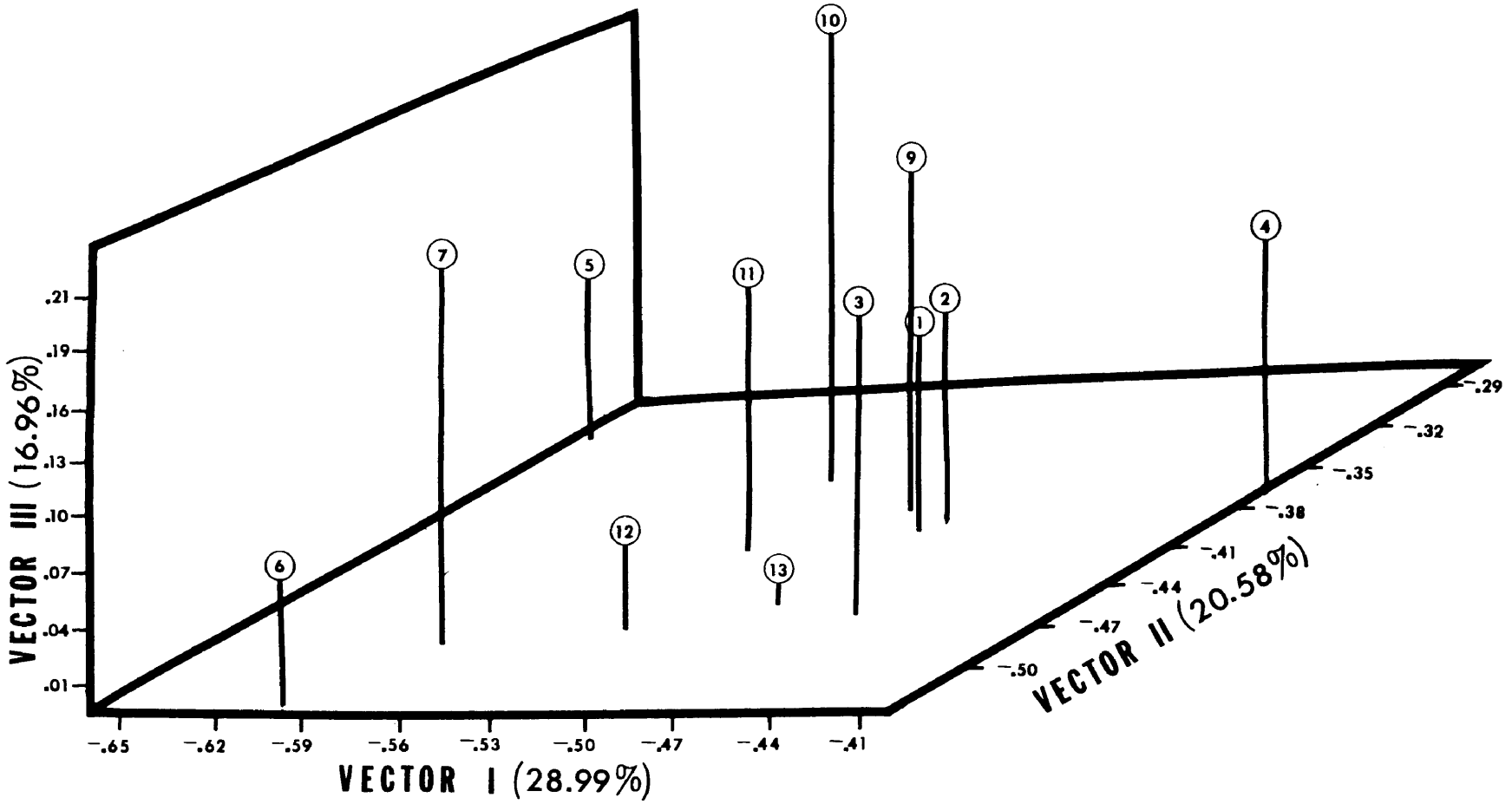


Figure 11. Projections on the first three canonical vectors of 12 samples of adult male Sceloporus olivaceus (ratios).

slightly discriminates sample 6 and Vector III does not appear to discretely discriminate the samples.

For females, Vector I was strongly influenced by R1 (34.63%), R13 (18.79%), and R6 (14.41%); Vector II by R1 (22.59%), R12 (13.45%), and R13 (11.99%); Vector III by R1 (37.19%), R6 (16.91%), and R13 (14.42%) (see Table 17). Figure 12 depicts female samples in three-dimensional space. Vector I discriminates samples 6 and 9 while Vector II slightly discriminates samples 6 and 8.

In comparing the plots of each sex, sample 6 was the only sample which was consistently discriminated in both.

Cluster analysis by phenetic similarity was performed for all samples by sex using both meristic and morphometric characters. Correlation and distance matrices produced phenograms illustrating phenetic relationships among the 13 samples.

In males, the meristic character phenogram generated by the distance matrix produced a higher cophenetic correlation (0.879). The most disparate male OTU was sample 8, followed by sample 12 with the remaining samples forming a second cluster (Figure 13). The distance matrix phenogram for females (Figure 14) produced a cophenetic correlation of 0.888. The female OTUs separated into two groups, the most disparate being sample 6, followed by samples 7 and 8 with the other samples forming a second cluster. A comparison of the subclusters in both sexes fails to reveal groupings based on geographic affinities with the exception of samples 1, 2, and 3.

Correlation phenograms based on meristic characters produced cophenetic correlations of 0.911 in females and 0.747 in males. In

Table 17. Variable coefficients for canonical variates I, II, and III and the percent influence of each ratio on each vector for 12 samples of adult female Sceloporus olivaceus.

Ratio	Vector I		Vector II		Vector III	
	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence	Variable Coefficient	Percent Influence
R1	-8.6266	34.63	4.2963	22.59	5.6975	37.19
R2	1.5125	7.03	0.3665	2.23	-0.0166	0.13
R3	0.9235	1.56	-2.7294	6.04	-1.3023	3.58
R4	0.3214	2.65	-0.0562	0.61	0.0359	0.48
R5	0.0991	0.90	-0.0846	1.00	0.1607	2.37
R6	3.5899	14.41	-1.2515	6.58	2.5907	16.91
R7	-1.4920	8.20	-1.0469	7.53	-0.1512	1.35
R8	-0.0047	0.02	-0.3032	1.85	-0.5031	3.80
R9	-1.1629	4.92	-1.0882	6.02	1.2212	8.39
R10	-0.0576	2.32	-1.5792	8.30	-0.8439	5.51
R11	-1.1336	3.35	-3.0484	11.81	-0.5775	2.78
R12	0.4138	1.22	3.4729	13.45	-0.6450	3.10
R13	4.4470	18.79	2.1665	11.99	-2.0985	14.42

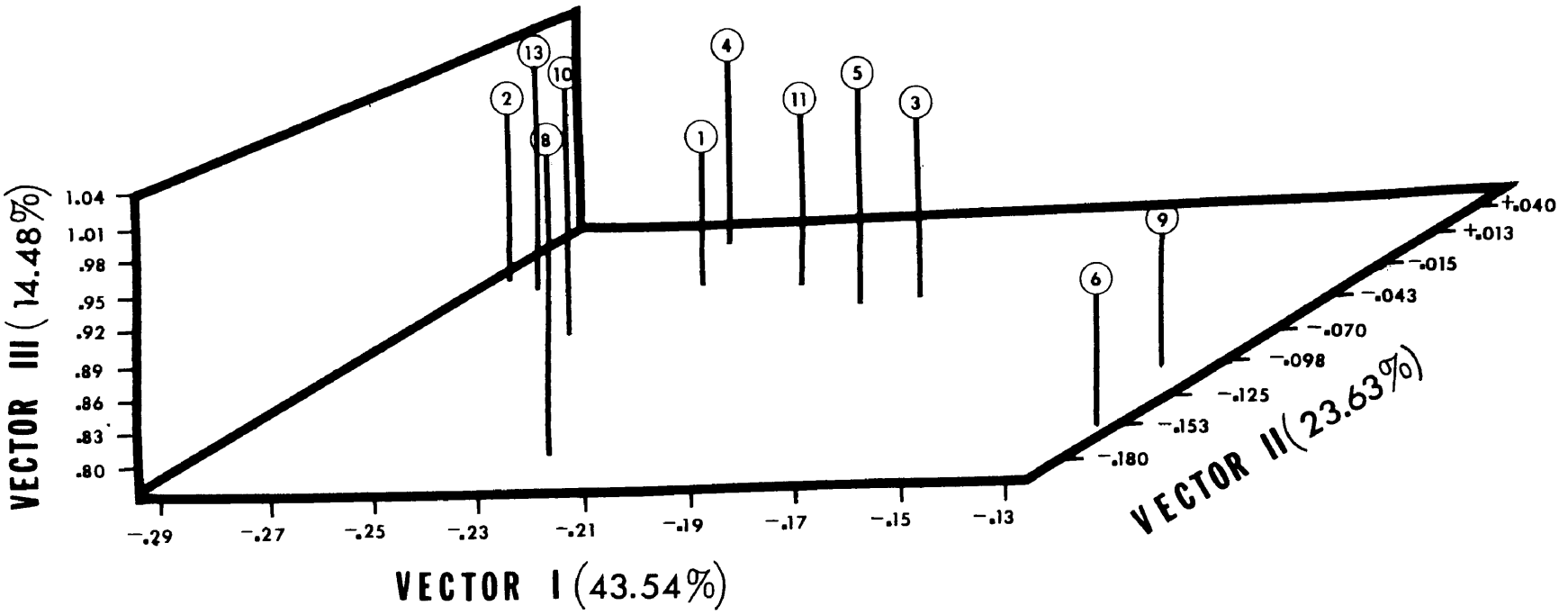


Figure 12. Projections on the first three canonical vectors of 11 samples of adult female Sceloporus olivaceus (ratios).

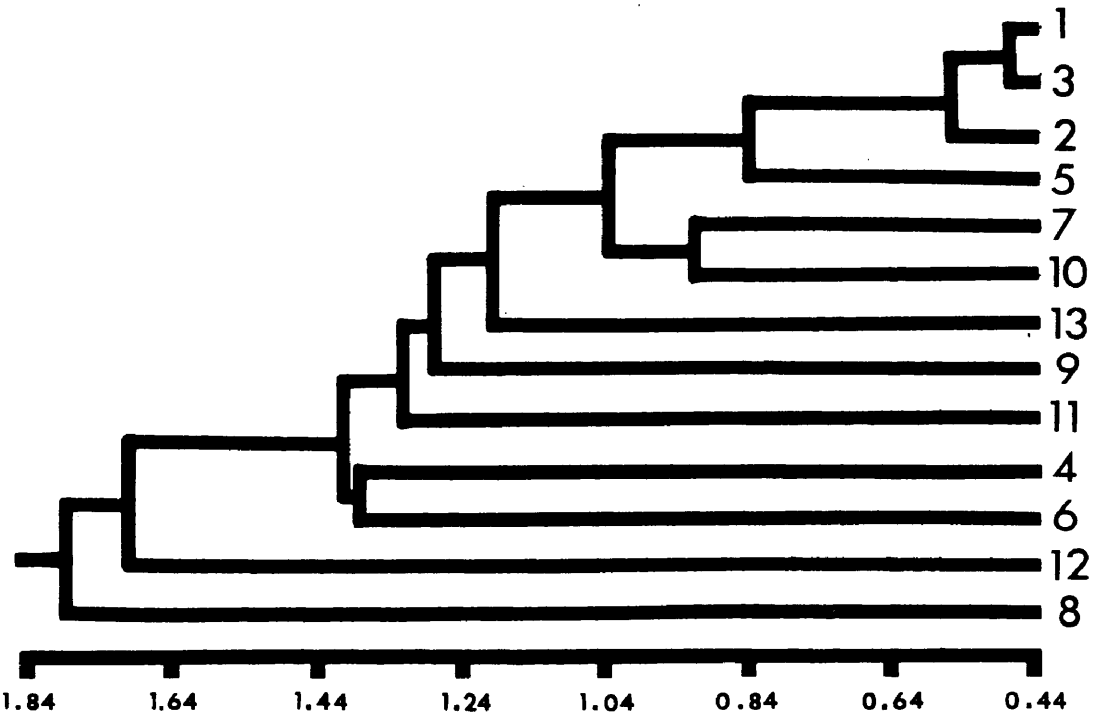


Figure 13. Phenogram generated from the meristic character distance matrix for male Sceloporus olivaceus. Numbers on the right designate sample area; the cophenetic correlation is 0.879.

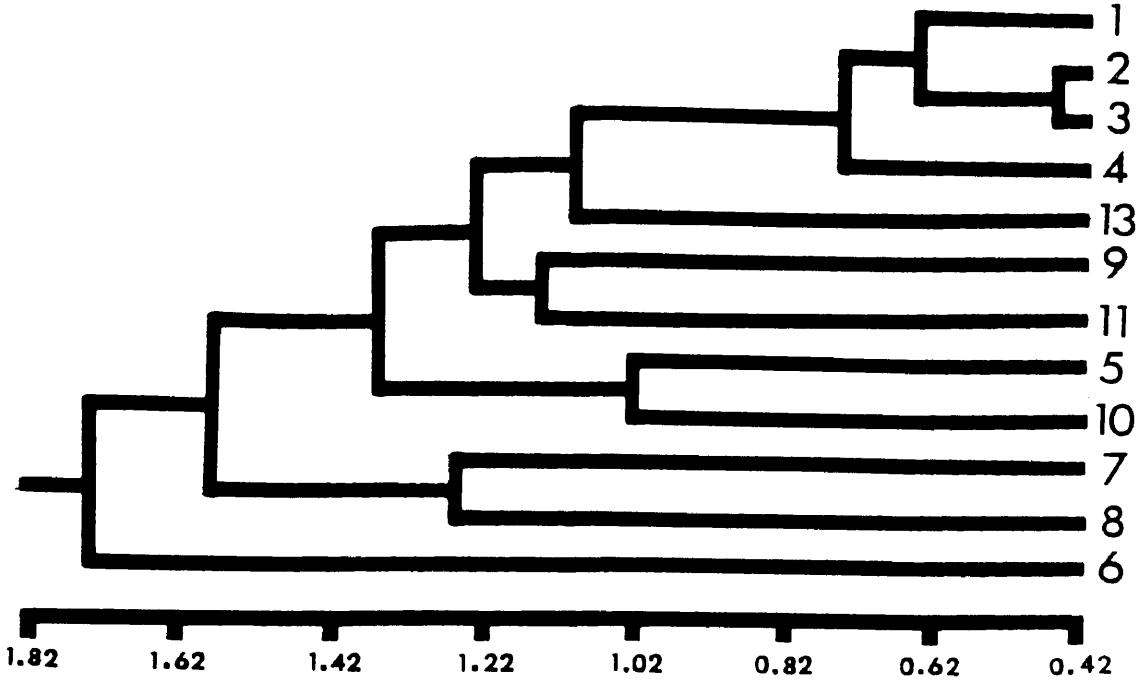


Figure 14. Phenogram generated from the meristic character distance matrix for female Sceloporus olivaceus. Numbers on the right designate sample areas; the cophenetic correlation is 0.888.

female OTUs, two groupings occur, one comprising samples 5, 10, and 7, 8 and all others forming a second cluster (Figure 15). Male OTUs form two groups, one comprising samples 5, 12, 6 and 7, 11, 13 with the others forming a second cluster (Figure 16). In comparing both phenograms, intersex differences are apparent with the exception of shared subclusters of samples 1, 2, 3, and 4.

Disparities in clustering patterns are evident in the morphometric distance phenograms of the sexes with no major clustering based on geographic proximity. Males (Figure 17), with a cophenetic correlation of 0.905, showed no major clusters but discriminated sample 8. Females (Figure 18), with a cophenetic correlation of 0.938, discriminated sample 7 from all others.

In comparing the distance phenograms of meristic and morphometric characters of both sexes, it appears that while some geographic groupings occur, there are major disparities in OTU groupings. These disparities would seem to indicate that geographic proximity is not a good indicator of phenetic similarity. Over all phenograms considered, sample 6 seems to show the highest diversification.

Allozyme Variation

Allele frequency data for all polymorphic loci for all samples (except sample 9) for *S. olivaceus* are summarized in Table 18. A total of 17 loci were analyzed; seven were monomorphic: LDH-2, MDH-2, IPO, α-GPD, XDH, PGM-1, and EST-4. PGM-1 and EST-4 were heterozygous in a single, different individual from one locality. The common

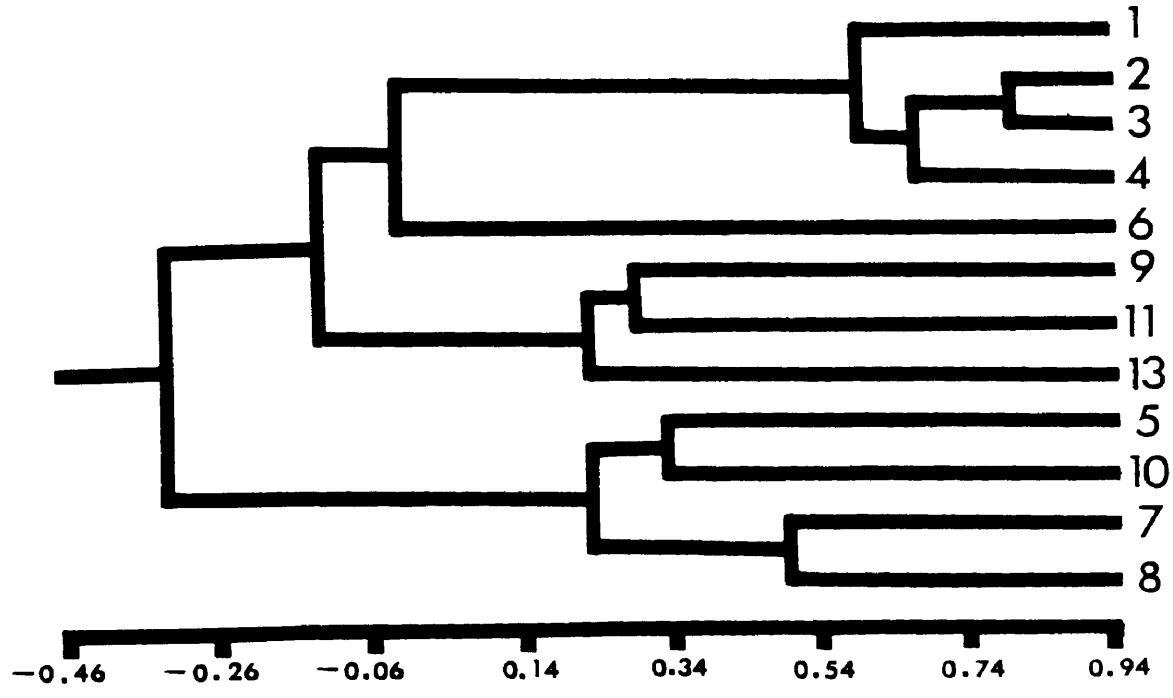


Figure 15. Phenogram generated from the meristic character correlation matrix for female Sceloporus olivaceus. Numbers on the right designate sample areas; the correlation coefficient is 0.911.

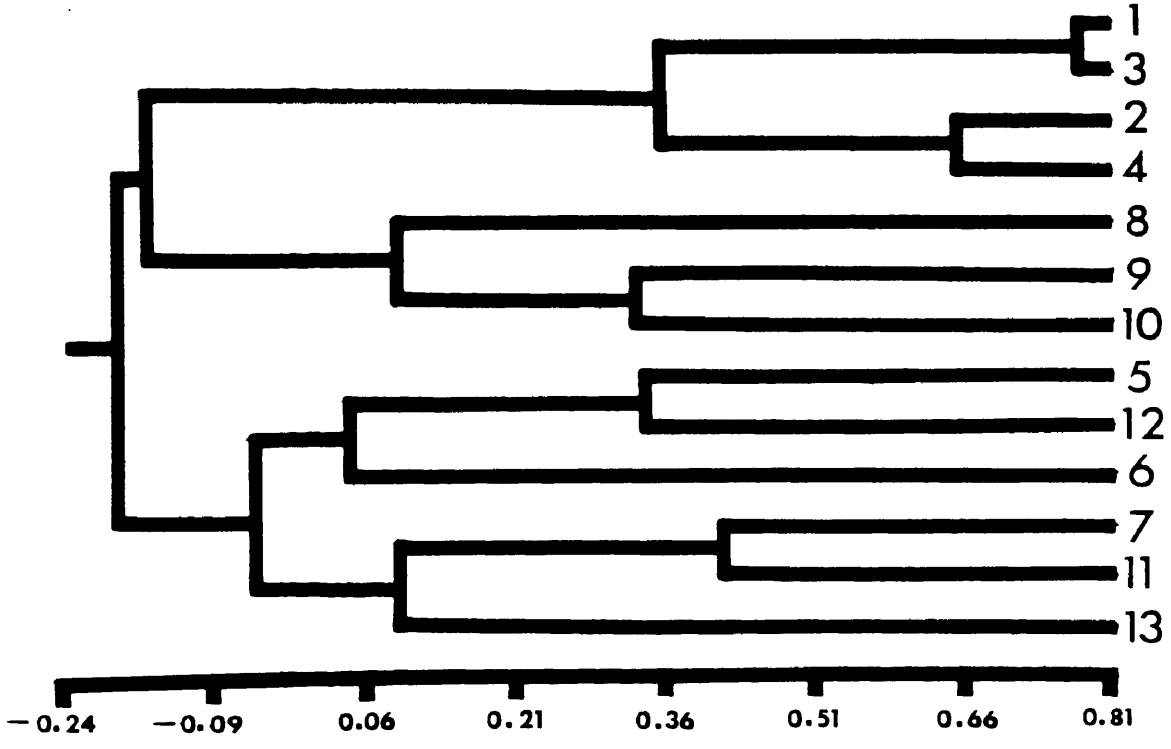


Figure 16. Phenogram generated from the meristic character correlation matrix for male Sceloporus olivaceus. Numbers on the right designate sample areas; the cophenetic correlation is 0.747.

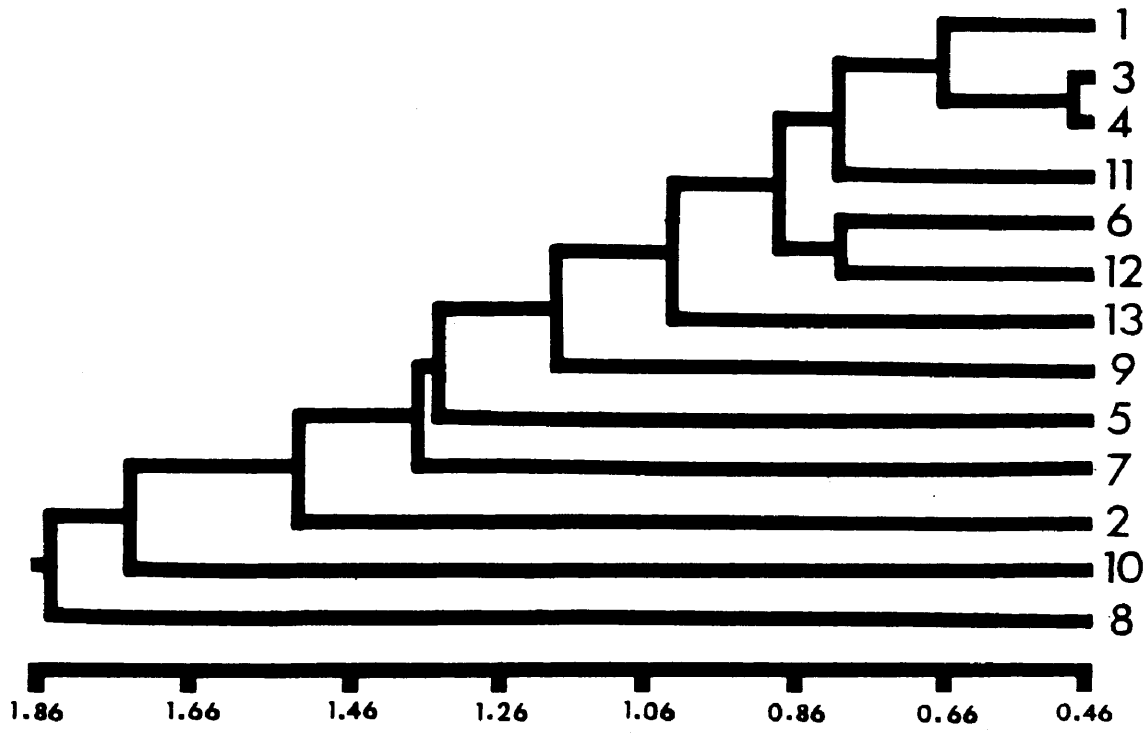


Figure 17. Phenogram generated from the morphometric character distance matrix for male Sceloporus olivaceus. Numbers on the right designate sample areas; the cophenetic correlation is 0.905.

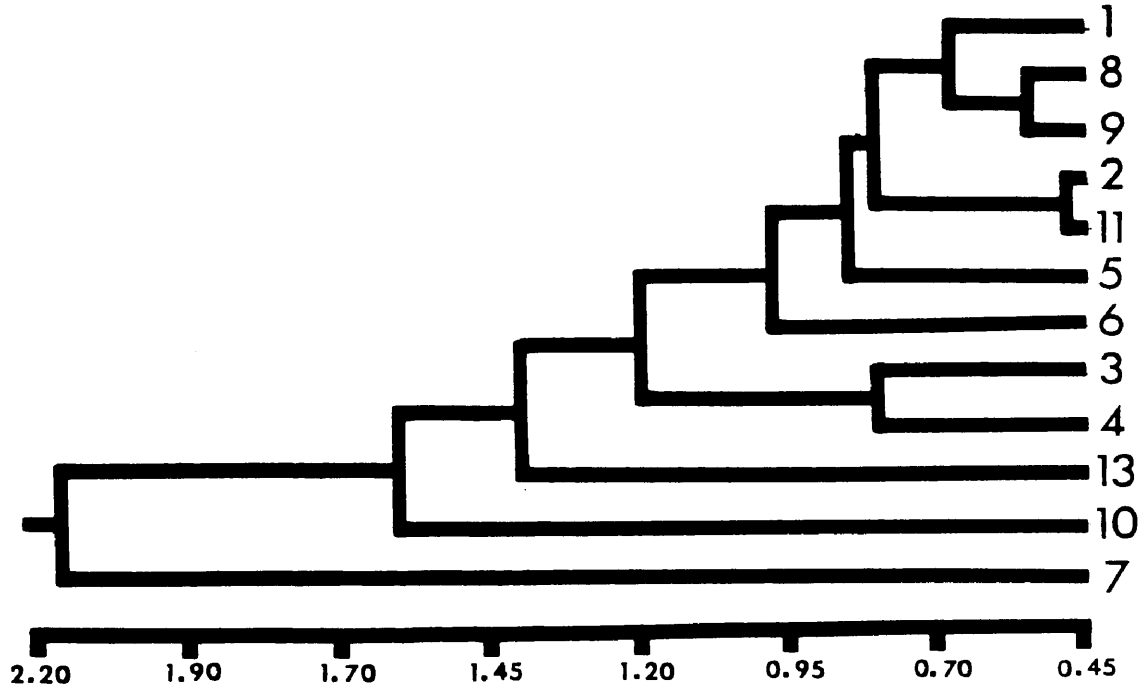


Figure 18. Phenogram generated from the morphometric character distance matrix for female Sceloporus olivaceus. Numbers on the right designate sample areas; the cophenetic correlation is 0.938.

Table 18. Allele frequencies for 10 polymorphic loci in 12 samples of Sceloporus olivaceus.

Locus	Sample 1	2	3	4	5	6	7	8	10	11	12	13
ME												
(N)	66	114	84	24	6	16	8	4	4	24	1	8
A	.030	.123	.012	.000	.000	.000	.000	.000	.000	.000	.000	.000
C	.811	.675	.756	.792	.667	.938	1.000	.875	1.000	1.000	1.000	.938
E	.159	.202	.232	.208	.333	.063	.000	.125	.000	.000	.000	.063
LDH-1												
(N)	72	135	94	24	6	16	8	5	4	24	4	9
B	.014	.044	.043	.042	.000	.000	.000	.000	.250	.083	.250	.111
D	.931	.930	.910	.896	1.000	.969	1.000	1.000	.625	.917	.750	.889
E	.056	.026	.048	.063	.000	.031	.000	.000	.125	.000	.000	.000
MDH-1												
(N)	73	135	94	24	6	16	8	5	4	24	4	9
A	.959	.978	1.000	.958	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	.041	.022	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000
GOT-1												
(N)	71	135	94	24	6	16	8	5	4	24	4	9
A	.000	.000	.005	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.993	.993	.968	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
D	.007	.007	.027	.000	.000	.000	.000	.000	.000	.000	.000	.000
GOT-2												
(N)	73	133	94	24	6	16	8	5	4	24	4	9
B	.918	.947	.957	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
C	.082	.053	.043	.083	.000	.000	.000	.000	.000	.000	.000	.000

Table 18. (Continued).

Locus	Sample 1	2	3	4	5	6	7	8	10	11	12	13
IDH												
(N)	52	112	76	22	6	15	8	3	3	10	4	8
A	.067	.107	.112	.114	.000	.800	.250	.333	.000	.350	.000	.500
D	.933	.893	.888	.886	1.000	.200	.750	.667	1.000	.650	1.000	.500
PGM-2												
(N)	73	132	91	24	6	16	8	5	4	23	4	9
A	.027	.008	.028	.042	.000	.000	.000	.100	.000	.043	.000	.000
D	.973	.992	.972	.958	1.000	1.000	1.000	.900	1.000	.957	1.000	1.000
EST-1												
(N)	73	133	94	24	6	16	8	5	4	24	4	9
A	.068	.090	.074	.083	.000	.313	.000	.000	.250	.000	.000	.167
B	.918	.823	.819	.688	.750	.531	1.000	.900	.625	.583	.250	.833
C	.014	.086	.106	.229	.250	.156	.000	.100	.125	.417	.750	.000
LAP												
(N)	73	134	93	24	6	16	8	5	4	24	4	9
A	.000	.000	.005	.104	.000	.216	.000	.000	.000	.000	.000	.222
B	1.000	.970	.973	.854	1.000	.781	1.000	1.000	1.000	1.000	1.000	.778
D	.000	.030	.022	.042	.000	.000	.000	.000	.000	.000	.000	.000
ADH												
(N)	74	135	90	24	6	16	8	5	4	23	4	9
A	1.000	.974	.950	.938	1.000	1.000	1.000	1.000	1.000	.674	1.000	.722
D	.000	.026	.050	.063	.000	.000	.000	.000	.000	.326	.000	.278

allele was fixed or predominant at most loci across all populations. The loci exhibited regional, populational, or discordant geographic allelic variation.

Regional variation between samples in Texas and Mexico was apparent in ME, MDH-1, GOT-1, GOT-2, and to some extent in LAP and ADH. The ME^{A} allele was present at a low average frequency (0.055) in three Texas samples (1, 2, 3) while being absent in Mexican samples. The ME^{E} allele exhibited a higher average frequency (0.200) in all Texas samples compared to 0.146 for Mexican samples 5, 6, 8, and 13. The $MDH\text{-}1^{B}$ allele was present at a low average frequency (0.035) in three Texas samples (1, 2, 4) and absent in Mexican samples. The GOT-1 and GOT-2 loci exhibited this same pattern of regional variation with $GOT\text{-}1^{D}$ and $GOT\text{-}2^{C}$ being present in Texas samples (3 and 1-4, respectively) at low frequencies and absent in Mexican populations. The LAP^{D} allele was present in three Texas samples (1, 2, 3) at low frequencies and absent in Mexican samples. The LAP^{A} allele was present at a low average frequency of 0.055 in two Texas samples (3, 4) and at a higher average frequency of 0.221 in two samples in Mexico. The ADH^{D} allele was present at a low average frequency of 0.046 in three Texas samples (2, 3, 4) and at a higher average frequency (0.302) in Mexican samples 11 and 13.

The IDH and EST-1 loci exhibited patterns of geographic variation within the Mexican samples. Samples 6 and 13 exhibited high frequencies (0.800 and 0.500 respectively) for the IDH^{A} allele compared to the average (0.229) of all other Mexican samples. Sample 12 exhibited a high frequency (0.750) of the $EST\text{-}1^{C}$ allele compared

to the average frequency (0.165) for all other samples. Samples 11 and 5 exhibited frequencies of 0.417 and 0.250 respectively, for the same EST-1^{C} allele. Sample 6 exhibited a high frequency (0.313) of EST-1^{A}. EST-1^{B} was present, common, or fixed for all other samples. The remaining loci showed little geographic differentiation between the samples.

Table 19 summarizes calculations of the proportion of loci heterozygous averaged over all individuals per sample (H), the average number of alleles per locus per sample (A), and the average proportion of polymorphic loci per sample (P). To better compare with calculations from other studies, P was calculated using 0.01(P') and 0.05(P") criteria.

Heterozygosity estimates over all 12 samples average 0.037 (0.010-0.068). The percentage of loci polymorphic (P) averaged 0.230 (0.06-0.41). The number of alleles per locus per sample (A) averaged 1.40 (1.06-1.94).

Table 20 summarizes the matrices of Nei's (1972) genetic distance (D) and Rogers' (1972) genetic similarity (S) calculated for all pairwise comparisons of samples. D values ranged from 0.001 to 0.066. Sample 6 exhibited the highest D values averaging 0.040 (0.016-0.066) over all samples. Sample 12 exhibited the next highest D values averaging 0.036 (0.020-0.066) over all samples. S values ranged from 0.889 to 0.984. Sample 6 exhibited the lowest S values averaging 0.914 (0.892-0.945) over all samples. Sample 12 exhibited the next lowest S values averaging 0.921 (0.889-0.961) over all samples.

Table 19. Genetic variation estimates for 12 samples of Sceloporus olivaceus including: mean heterozygosities ($\bar{H}$), mean number of alleles/locus/sample ($\bar{A}$), and the number of polymorphic loci/sample if (a) the common allele 0.99 (P'), and (b) if the common allele 0.95 (P").

Parameter	Sample 1	2	3	4	5	6	7	8	10	11	12	13
$\bar{H}$	.028	.034	.049	.052	.010	.068	.015	.038	.029	.038	.029	.048
$\bar{A}$	1.65	1.76	1.94	1.71	1.12	1.35	1.06	1.24	1.24	1.29	1.12	1.35
P'	.41	.47	.65	.53	.12	.29	.06	.24	.12	.29	.12	.35
P"	.29	.29	.29	.41	.12	.24	.06	.24	.12	.24	.12	.35

Table 20. Rogers (1972) genetic similarity (S, above diagonal) and Nei (1972) genetic distance (D, below diagonal) between all pairwise combinations of 12 samples of Sceloporus olivaceus.

	Sample											
	1	2	3	4	5	6	7	8	10	11	12	13
1	----	.976	.975	.967	.961	.906	.961	.961	.945	.919	.922	.919
2	.002	----	.984	.968	.966	.909	.954	.954	.942	.923	.920	.923
3	.001	.001	----	.974	.964	.908	.952	.957	.942	.929	.921	.925
4	.005	.003	.002	----	.955	.916	.937	.944	.937	.930	.921	.924
5	.005	.003	.003	.004	----	.906	.951	.953	.948	.923	.936	.906
6	.047	.043	.041	.037	.054	----	.925	.928	.913	.914	.892	.945
7	.005	.008	.007	.010	.014	.033	----	.976	.946	.943	.926	.936
8	.006	.007	.005	.008	.012	.026	.002	----	.932	.946	.914	.936
10	.012	.013	.011	.011	.017	.052	.017	.020	----	.927	.961	.913
11	.024	.021	.018	.015	.024	.030	.018	.015	.024	----	.928	.946
12	.037	.033	.031	.022	.026	.066	.043	.039	.020	.023	----	.889
13	.023	.021	.019	.019	.033	.016	.014	.013	.030	.014	.056	----

The UPGMA option clustered the matrix of Rogers' (1972) genetic similarity with a cophenetic correlation of 0.874 (Figure 19). The samples form a dichotomy at the 0.92 level with little geographic affinity. Examination of the subclusters reveals some geographic affinities clustering the Texas samples (1-4) with sample 5 and samples 8 and 7. The remaining groupings often cluster geographically separated samples (i.e. sample 6 with samples 11 and 13). In addition, the UPGMA option was used to cluster matrices of Nei's (1978) unbiased genetic identity, Nei's (1978) unbiased genetic distance, Nei's (1978) unbiased minimum distance, Nei's (1972) minimum distance, Rogers' (1972) genetic distance, modified Rogers distance (Wright, 1978), Nei's (1972) genetic identity, and Nei's (1972) genetic distance.

Figure 20 depicts a phenogram of modified Rogers distance (Wright, 1978); the cophenetic correlation is 0.915. Some geographic affinity is indicated with samples 1-5 and samples 7 and 8 clustering together, while the remaining subclusters indicate little geographic affinity. Samples 6 and 12 tend to cluster away from the remaining samples. This pattern is similar to the other phenograms produced from the different methods mentioned above.

Table 21 summarizes the means for inbreeding coefficient due to non-random mating variation within samples (Fis); allelic fixation index due to weighted effects of non-random mating within samples (Fit); and fixation index of alleles between samples (Fst) for each polymorphic locus across all samples of *S. olivaceus*. The mean Fis for the individual loci across all samples is 0.562 with a range of

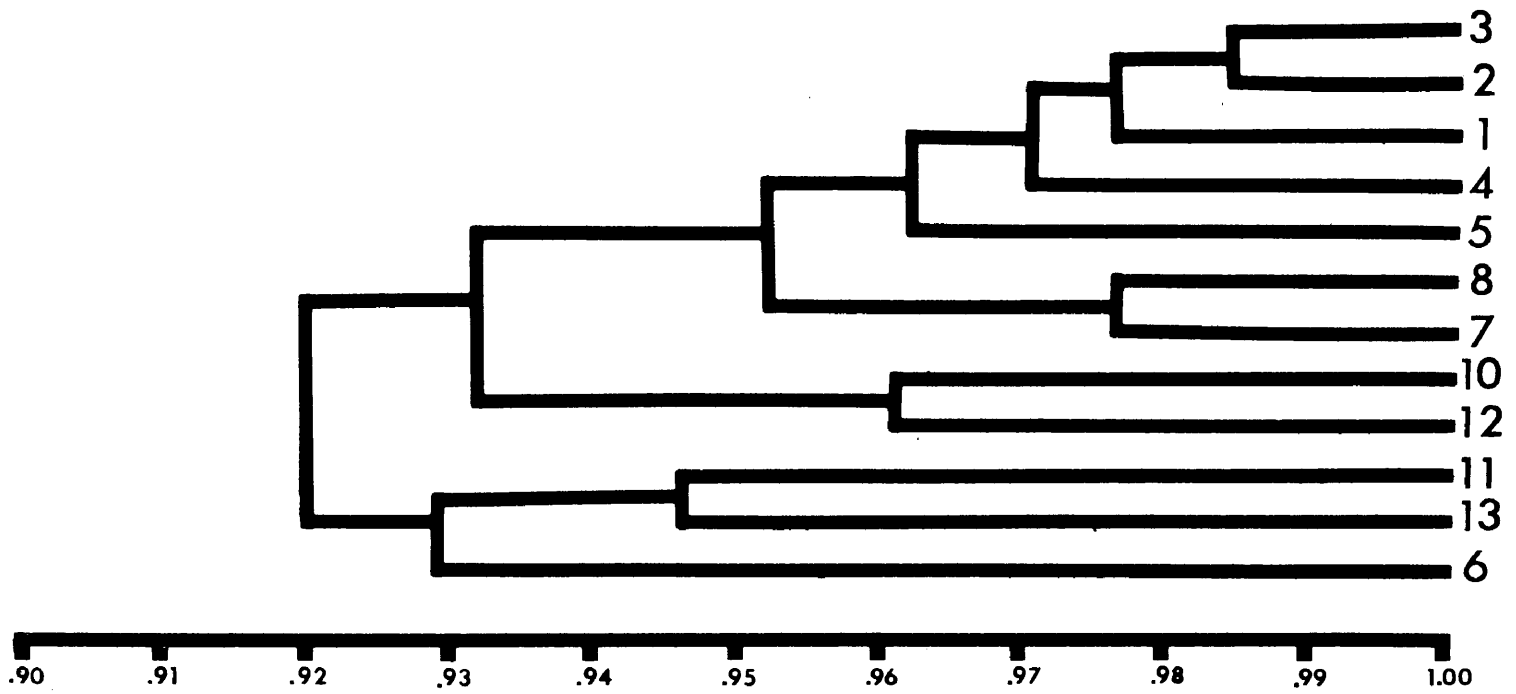


Figure 19. Phenogram generated from the Rogers (1972) genetic similarity matrix. Numbers on the right designate sample areas; the cophenetic correlation is 0.874.

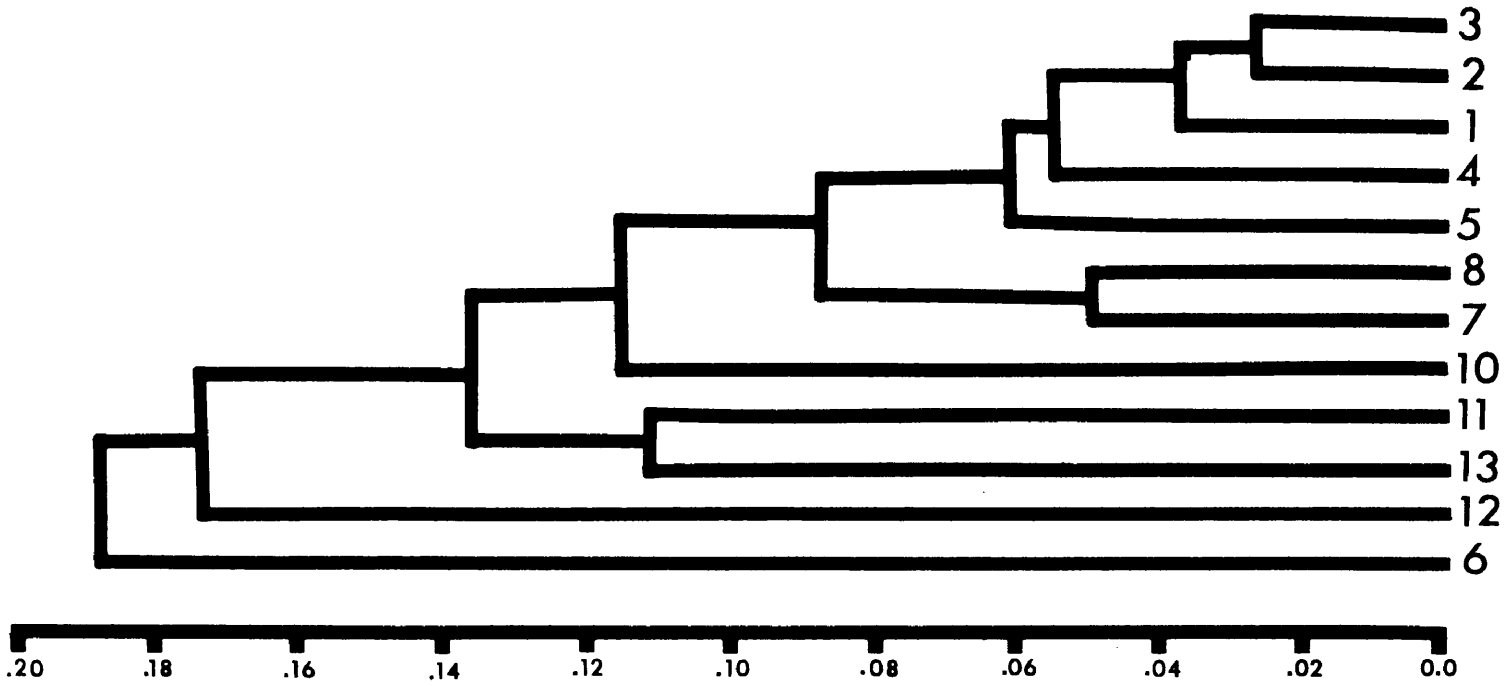


Figure 20. Phenogram generated from the modified Rogers distance matrix (Wright, 1978). Numbers on the right designate sample areas; the cophenetic correlation is 0.915.

Table 21. Summary of F-statistics (Wright, 1978) for all polymorphic loci in 12 samples of Sceloporus olivaceus.

Locus	F(IS)	F(IT)	F(ST)
ME	.387	.461	.121
LDH-1	.649	.688	.111
MDH-1	1.000	1.000	.029
GOT-1	.142	.157	.018
GOT-2	1.000	1.000	.049
IDH	.488	.650	.316
PGM-2	.546	.565	.042
EST-1	.374	.507	.212
LAP	.632	.683	.139
ADH	.406	.530	.208
$\bar{X}$	.562	.624	.125

0.142 to 1.000, while the mean for Fit is 0.624 with a range of 0.157 to 1.000. Fst values ranged from 0.029 to 0.316 with a mean of 0.125 indicating a relatively low level of genetic subdivision within the species.

Interspecific Variation

S. spinosus, *S. cautus*, and *S. cyanogenys* were compared electrophoretically to *S. olivaceus*. Table 22 summarizes the allele frequencies for all loci for the four species. Of the 17 loci analyzed, four (MDH-2, IPO, α-GPD, and XDH) were fixed for a single electromorph in all four species. At MDH-1 and EST-4, the common allele in *S. olivaceus* was fixed in *S. spinosus*, *S. cautus*, and *S. cyanogenys*. *S. spinosus* displayed two electromorphs (PGM-$2^{C,F}$) not found in *S. olivaceus*. *S. cautus* exhibited five electromorphs not found in *S. olivaceus*, (ME^{B}, $IDH^{C,E}$, and $ADH^{B,E}$) *S. cyanogenys* displayed 12 electromorphs not found in *S. olivaceus*, (ME^{D}, LDH-$1^{A,C}$, LDH-2^{A}, GOT-1^{C}, GOT-2^{D}, IDH^{B}, PGM-1^{C}, PGM-2^{C}, LAP^{C}, and $ADH^{C,F}$).

Table 23 summarizes the matrices of Nei's (1972) genetic distance (D) and Rogers' (1972) genetic similarity (S) calculated for all pairwise comparisons of the four species. S values for *S. spinosus* averaged 0.898 (0.869-0.914) over all samples of *S. olivaceus* and in two cases *S. spinosus* was more similar to *S. olivaceus* than samples within *S. olivaceus*. *S. cautus* S values averaged 0.810 (0.793-0.839) over all samples of *S. olivaceus*. S values for *S. cyanogenys* compared to *S. olivaceus* ranged from 0.383 to 0.430 and averaged 0.415.

Table 22. Allele frequencies for 17 loci in 12 samples of Sceloporus olivaceus and one sample each of Sceloporus spinosus, Sceloporus cautus, and Sceloporus cyanogenys.

	Sample														
Locus	1	2	3	4	5	6	7	8	10	11	12	13	spin	caut	cyan
ME															
(N)	66	114	84	24	6	16	8	4	4	24	1	8	9	23	16
A	.030	.123	.012	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000	.000
C	.811	.675	.756	.792	.667	.938	1.000	.875	1.000	1.000	1.000	.938	.944	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
E	.159	.202	.232	.208	.333	.063	.000	.125	.000	.000	.000	.063	.056	.000	.000
LDH-1															
(N)	72	135	94	24	6	16	8	5	4	24	4	9	9	30	17
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.059
B	.014	.044	.043	.042	.000	.000	.000	.000	.250	.083	.250	.111	.000	.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.941
D	.931	.930	.910	.896	1.000	.969	1.000	1.000	.625	.917	.750	.889	1.000	1.000	.000
E	.056	.026	.048	.063	.000	.031	.000	.000	.125	.000	.000	.000	.000	.000	.000
LDH-2															
(N)	73	135	94	24	6	16	8	5	4	24	4	9	9	30	17
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000
MDH-1															
(N)	73	135	94	24	6	16	8	5	4	24	4	9	9	25	17
A	.959	.978	1.000	.958	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
B	.041	.022	.000	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
MDH-2															
(N)	73	135	94	24	6	16	8	5	4	24	4	9	9	25	17
B	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 22. (Continued).

Locus	Sample 1	2	3	4	5	6	7	8	10	11	12	13	spin	caut	cyan
GOT-1															
(N)	71	135	94	24	6	16	8	5	4	24	4	9	9	30	17
A	.000	.000	.005	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	.993	.993	.968	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
D	.007	.007	.027	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
GOT-2															
(N)	73	133	94	24	6	16	8	5	4	24	4	9	9	30	17
B	.918	.947	.957	.917	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.000
C	.082	.053	.043	.083	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
D	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
IDH															
(N)	52	112	76	22	6	15	8	3	3	10	4	8	9	15	14
A	.067	.107	.112	.114	.000	.800	.250	.333	.000	.350	.000	.500	.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.632	.000
D	.933	.893	.888	.886	1.000	.200	.750	.667	1.000	.650	1.000	.500	1.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.368	.000
PGM-1															
(N)	73	132	91	24	6	16	8	5	4	23	4	9	9	30	17
A	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.033	.000
B	1.000	1.000	.989	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	.967	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
D	.000	.000	.011	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000

Table 22. (Continued).

Locus	Sample 1	2	3	4	5	6	7	8	10	11	12	13	spin	caut	cyan
PGM-2															
(N)	73	132	90	24	6	16	8	5	4	23	4	9	9	30	17
A	.027	.008	.028	.042	.000	.000	.000	.100	.000	.043	.000	.000	.000	.033	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.111	.000	.000
D	.973	.992	.972	.958	1.000	1.000	1.000	.900	1.000	.957	1.000	1.000	.000	.967	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.889	.000	.000
IPO															
(N)	73	132	91	24	6	16	8	5	4	23	4	9	9	30	17
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
-GPD															
(N)	74	135	94	24	6	16	8	5	4	24	4	9	9	30	17
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
EST-1															
(N)	73	133	94	24	6	16	8	5	4	24	4	9	9	29	17
A	.068	.090	.074	.083	.000	.313	.000	.000	.250	.000	.000	.167	.222	.000	.000
B	.918	.823	.819	.688	.750	.531	1.000	.900	.625	.583	.250	.833	.778	.517	.882
C	.014	.086	.106	.229	.250	.156	.000	.100	.125	.417	.750	.000	.000	.483	.118
EST-4															
(N)	53	124	94	23	6	16	8	5	4	24	4	9	9	30	17
A	.000	.000	.011	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
B	1.000	1.000	.989	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
XDH															
(N)	73	134	94	24	6	16	8	5	4	24	4	9	9	30	17
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table 22. (Continued).

Locus	Sample 1	2	3	4	5	6	7	8	10	11	12	13	spin	caut	cyan
LAP															
(N)	73	134	93	24	6	16	8	5	4	24	4	9	9	30	17
A	.000	.000	.005	.104	.000	.219	.000	.000	.000	.000	.000	.222	.000	.000	.000
B	1.000	.970	.973	.854	1.000	.781	1.000	1.000	1.000	1.000	1.000	.778	1.000	1.000	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	1.000
D	.000	.030	.022	.042	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000
ADH															
(N)	74	135	90	24	6	16	8	5	4	23	4	9	9	23	17
A	1.000	.974	.950	.938	1.000	1.000	1.000	1.000	1.000	.674	1.000	.722	1.000	.000	.000
B	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.848	.000
C	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.971
D	.000	.026	.050	.063	.000	.000	.000	.000	.000	.326	.000	.278	.000	.000	.000
E	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.152	.000
F	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.029

Table 23. Rogers (1972) genetic similarity (S, above diagonal) and Nei (1972) genetic distance (D, below diagonal) averaged for all pairwise combinations of 12 samples of Sceloporus olivaceus and one sample each of Sceloporus spinosus, Sceloporus cautus, and Sceloporus cyanogenys.

		spinosus	cautus	cyanogenys
olivaceus	S	0.898	0.810	0.415
	D	0.072	0.175	0.889
spinosus	S		0.755	0.407
	D		0.257	0.903
cautus	S			0.406
	D			0.907

The matrix of Rogers' (1972) genetic distances between OTUs was used to produce four distance Wagner trees; a midpoint rooted tree and three outgroup rooted trees for the four species. The outgroups included *S. spinosus*, *S. cautus*, and *S. cyanogenys*. The four trees were of identical lengths (1.036) and produced equal goodness-of-fit statistics: Farris (1972) "F"=2.147, Prager and Wilson (1976) "F"=13.346, Percent Standard Deviation (Fitch and Margoliash, 1967)=22.442, the cophenetic correlation was 0.996. Each tree estimates that *S. cyanogenys* is the oldest lineage. Subclusters of *S. olivaceus* are generally similar depending on the outgroup involved. Samples 1-4, 10 and 12, 7 and 8, and 6 and 13 all show the same clustering pattern in all trees.

Figure 21 depicts a Wagner tree with *S. spinosus* as an outgroup. *S. cautus* and *S. cyanogenys* branch with sample 11 and appear to be most divergent. Figure 22 depicts a Wagner tree with *S. cautus* as an outgroup, *S. cyanogenys* branches outside *S. olivaceus*, and *S. spinosus* branches with samples 10 and 12.

Figure 23 depicts a Wagner tree with *S. cyanogenys* as an outgroup (the midpoint rooted tree produced an identical phenogram). *S. cautus* branched outside *S. olivaceus* samples and *S. spinosus* clusters with *S. olivaceus* samples 10 and 12.

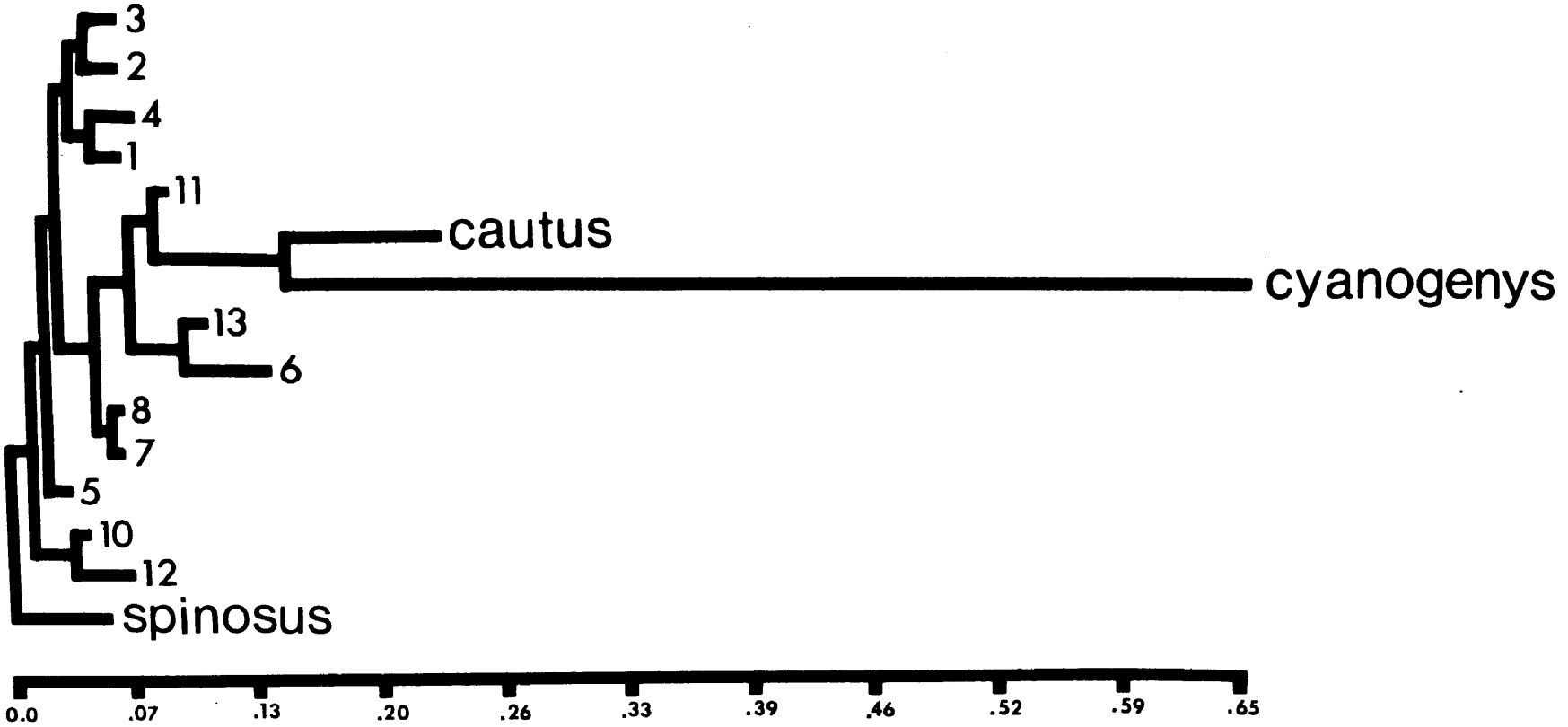


Figure 21. Wagner tree generated from Rogers (1972) genetic distances; Sceloporus spinosus as the outgroup.

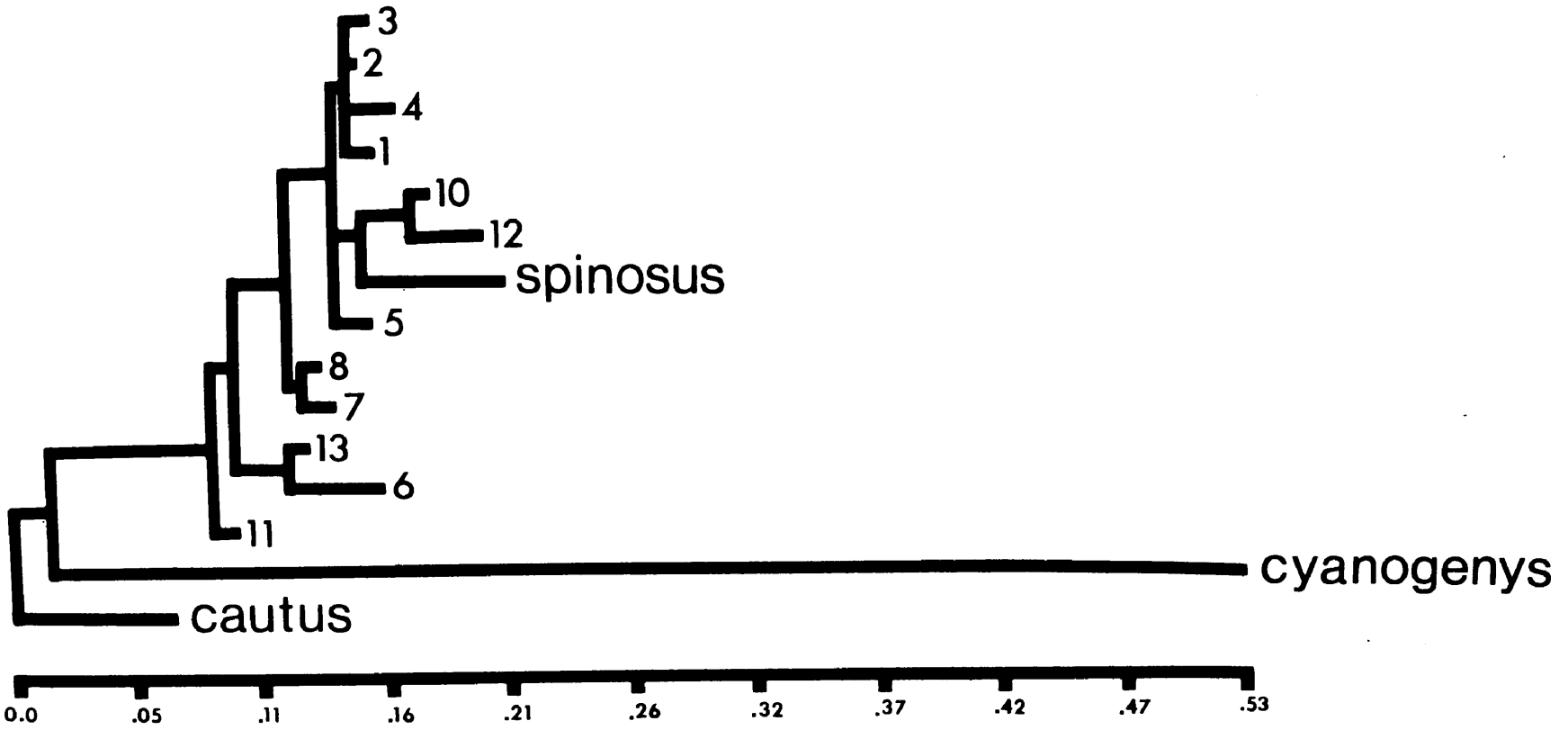


Figure 22. Wagner tree generated from Rogers (1972) genetic distances; Sceloporus cautus as the outgroup.

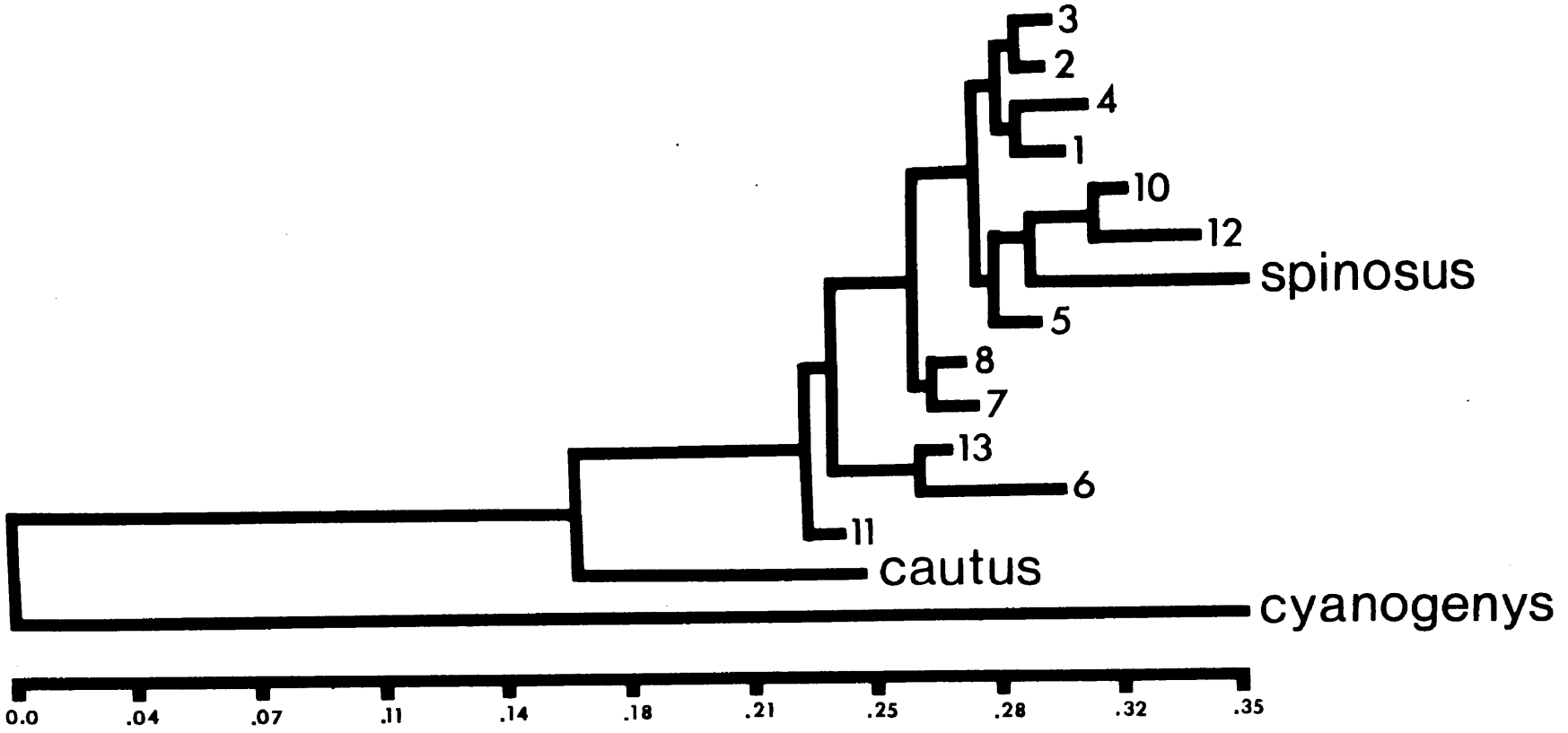


Figure 23. Wagner tree generated from Rogers (1972) genetic distances; Sceloporus cyanogenys as the outgroup.

DISCUSSION

Chromosomal Analysis

No detectable chromosomal polymorphisms were found throughout the 270 specimens examined. This particular karyotype (2n=22) contributes to the confusing relationships between the *spinosus* and *undulatus* groups. Cole (1970) discussed the karyotypes of the *spinosus* group and designated four general types within the group: the *melanorhinus*-type (2n=40), the *orcutti*-type (2n=34), the *magister*-type (2n=26), and the *lundelli*-type (2n=22). Cole feels these groupings reflect phylogenetic affinities and that the *lundelli*-type represents the more derived form. The *lundelli*-type karyotype is characterized by six pairs of macrochromosomes and five pairs of smaller elements. Macrochromosomes 1, 3, 4, and 5 are metacentric while 2 and 6 are submetacentric. Number 2 usually bears a terminal satellite. The smaller elements are usually metacentric (pairs 7-10) or subtelo- or submetacentric (pair 11). Most variation between the species of the *lundelli*-type occurs in the five pairs of smaller elements. Species representing the *lundelli*-type are *S. lundelli*, *S. edwardtaylori*, *S. horridus*, *S. spinosus*, and *S. olivaceus*.

S. lundelli is notably distinct in that it possesses an X-Y type of sex correlated chromosomes (pair 7). *S. edwardtaylori* lacks the terminal satellite on pair 2 but possesses an inconspicuous satellite on one arm of pair 8. This is probably the result of a translocation of satellite chromatin from pair 2. *S. olivaceus* possesses chromosomes nearly identical to *S. lundelli* lacking only the sex

chromosomes (pair 7 is homomorphic metacentric). *S. spinosus* is characterized by two karyotypes which reflect a geographic correlation. In this species, the karyotype is similar to *S. olivaceus* except in *S. spinosus apicalis* and *S. spinosus caeruleopunctatus* pair 9 is subtelocentric while *S. spinosus spinosus* is distinguished by a subtelocentric pair 7. *S. horridus* possesses two karyotypes which appear to be geographically correlated, both similar to *S. spinosus* but differing in centromere position of pair 7.

Cole (1972) and Sites and Haiduk (1979) described the karyotypes of the six species of the *undulatus* group and there are striking similarities with the *lundelli*-type of the *spinosus* group. The karyotypes of the six species are characterized by 2n=22 with six pairs of macrochromosomes and five pairs of smaller elements. Pairs 1, 3, 4, and 5 are metacentric and pairs 2 and 6 are submetacentric. The smaller elements are meta-, submeta-, or telocentric. Number 2 usually bears a terminal satellite present in all but one subspecies of *S. undulatus*. All variation appears to be in the morphology of pair 7; metacentric in *S. cautus* and *S. virgatus*, submetacentric in *S. woodi*, telocentric in *S. occidentalis*, and meta-, submeta-, subtelo-, and telocentric in the polytypic *S. undulatus*.

The chromosome morphology of the *lundelli*-type and the *undulatus* group are quite similar. Pairs 1, 3, 4, and 5 are metacentric and 2 and 6 are submetacentric with pair 2 usually bearing a terminal satellite in both. Most chromosome variation occurs in the centromere position of pair 7. Gross morphological similarities are apparent as well as noted by Ferguson (1982) which may indicate

taxonomic relatedness. Both *undulatus* and *spinosus* groups would be better understood with a detailed electrophoretic analysis and the refinement of differentially stained chromosome techniques.

Population Structure and Allozyme Analysis

One of the most comprehensive detailed populational studies on a sceloporine lizard was Blair's (1960) work on a population of *S. olivaceus* near Austin, Texas. This long term study provided important results on the organization of and the adaptation at the populational level, portions of which are summarized below.

Density of lizards was found to be related to the number of suitable trees in the area. Home ranges tended to be small encompassing a modal tree and several other less preferred sites. Males were found to be more active and have larger home ranges than females who were more sedentary.

This population maintained itself at a fairly steady level with an average breeding population of 17.8 to 25.2 lizards per acre on the ten acre study area. Females significantly outnumbered males indicating differential survival between the sexes which may be behaviorally related. Yearly turnover was high with 78.2% of the females and 82.5% of the males requiring replacement.

Yearly potential production was high with the number of eggs in a brood dependent on the size and age of the females. Older females may lay up to four broods per season. This population produced an average of 3016 (1958-4029) eggs a year during the five year study period. Approximately 75-78% of the potential broods failed due to

nest predation, infertility, or other reasons. In addition, 80.2 to 86.6% of the newly hatched lizards were lost to juvenile mortality as a result of predation, accidents, or other reasons. Only 2.5 to 5.5% of the potential brood survived to reach sexual maturity.

Most movements of adults were confined to home ranges. Nesting forays by females occurred both outside and inside the females home range with the female always returning to her home range. Adults tended to remain within their home range, most dispersal was by those juveniles who did not replace the parental population. With the high annual turnover of adults, most juveniles remained in the population with a small percentage dispersing to other suitable habitat. Direction of dispersal was not random but tended to follow suitable habitat avoiding dense thickets and ground cover, plowed fields, and roads.

Kerster (1964), based on Blair's populational data, estimated the effective population size (Ne) for *S. olivaceus*. Neighborhood size was estimated to be 10 hectares and the species range about 10 neighborhoods in area with 5000 neighborhood radii in extreme length. Ne was estimated to be 225-270 lizards. Kerster further noted the genetically important dispersal movements were the female nesting excursions and juvenile home range changes. He concluded that the breeding structure of *S. olivaceus* provides for faster evolution than panmixia.

Allozymic analysis of *S. olivaceus* populations reveals interesting results and supports Blair's (1960) work and Kerster's (1964) findings that the species is characterized by a large Ne. The

probablility of an individual being autozygous as a result of random gametes from two different sub-populations (Fst) of *S. olivaceus* is 0.125. While high Fst values indicate genetic subdivision, a low Fst value reflects a relatively high level of gene flow between the samples suggesting a large Ne. The genetically important dispersals by the small percentage of surviving juveniles and nesting females is apparently sufficient to maintain a high level of gene flow between populations. As noted by Schwartz and Armitage (1980) moderate levels of migration between demes can limit genetic differentiation between populations even in the socially structured marmot. For comparison, Table 24 depicts Fst values for various chromosomally monomorphic and polymorphic vertebrates.

The average inbreeding coefficient (Fis, the probablility that an individual is autozygous) for *S. olivaceus* is 0.562 and may be indicative of high inbreeding. Further, significant deviations from Hardy-Weinberg expectations in the form of heterozygote deficiencies can be accounted for by inbreeding or the Wahlund effect (the pooling of equilibrium populations that differ in allele frequency) (Patton and Fedor, 1981). Although Blair (1960) noted a high annual turnover and subsequent replacement by juveniles of the species, the amount of inbreeding is not known. Considering the size of the sample areas, the Wahlund effect probably contributed to this heterozygote deficiency.

A large Ne estimate for *S. olivaceus* is not only supported by a low Fst value but also a low D value. In general, species with a small Ne are characterized by low H and large D values while species

Table 24. Average Fst values for chromosomally monomorphic and polymorphic vertebrates (from Sites and Greenbaum, 1983).

Species	Fst	Cytotypes Sampled	Populations	Source
Sceloporus olivaceus	.125	1	12	This study
Sceloporus grammicus	.153(.099)	3	13(12)	Sites and Greenbaum, (1983)
Proechimys guairae	.139	4	5	Benado et al., (1979)
Peromyscus maniculatus	.159	1	18	Avise et al., (1979)
Uta stansburiana	.232	1	17	McKinney et al., (1972)
Thomomys talpoides	.387	6	10	Nevo et al., (1974)
Thomomys bottae	.412	1	23	Patton and Yang, (1977)
Sceloporus grammicus	.444	2	4	Hall and Selander, (1973)
Aneides flavipunctatus	.47(.28)	1	22(17)	Larson, (1980)
Cnemidophorus gularis	.589	-	24	Hanks, (1983)
Plethodon dorsalis	.737	1	27	Larson and Highton, (1978)

with a large Ne are characterized by high H and low D values. The average genetic distance for *S. olivaceus* (D=0.020) is low and comparable to values reported for *S. grammicus* (D=0.021-0.035) (Sites, 1980). This low distance value indicates little genetic differentiation between the samples. H for *S. olivaceus* is 0.037, low for most reported reptiles and may be compared to *S. grammicus* with an H=0.066-0.106 (Sites, 1980). Other examples include *Cnemidophorus tigris* with the highest reported average heterozygosity (H=0.146) (Gorman *et al.*, 1977), *Uta stansburiana*, H=0.055 (Soule and Yang, 1973) and H=0.048 (McKinney *et al.*, 1972), and *S. graciosus*, H=0.020 (Tinkle and Selander, 1973).

The relationship between Ne and H can be somewhat paradoxical. This has been illustrated by Patton and Fedor (1981) in the pocket gopher *Thomomys bottae* in which they observed populations characterized by small Ne and high individual heterozygosity. Although large Ne organisms are generally characterized by high H values, the low H value for *S. olivaceus* is a strong indication of a recent reduction in population size or a bottleneck. Low H has been reported in post-founder populations in the lizards, *Anolis* (Webster *et al.*, 1972 Gorman and Kim, 1975; Gorman *et al.*, 1978), *Uta stansburiana* (Soule and Yang, 1973), the cave fish *Astyanax* (Avise and Selander, 1972), and the pocket gopher *Geomys* (Penny and Zimmerman, 1976, Selander *et al.*, 1974). Wright (1931) notes that when a species population size is reduced suddenly, the average heterozygosity is expected to decline, with the rate of decline dependent on Ne and r, the rate of increase. As population size increases following the

bottleneck, H is expected to increase as well due to new mutations. Nei *et al*. (1975) note that once H is reduced to a low level, a long period of time is required for the H to reach its original or new level. Further, if the rate of population growth is high, a high level of heterozygosity can be maintained even with extreme bottlenecks.

The intrinsic rate of population growth following the bottleneck in *S. olivaceus* is unknown. However, if it is assumed that the rate of population growth is high, the loss of heterozygosity occurs in the early generations and as population size reaches a certain level, heterozygosity no longer decreases (Nei *et al*., 1975). Considering the current distribution and population size of *S. olivaceus*, a high rate of population growth would indicate that the original level of H was also low and that the current level may be approaching equilibria. On the other hand, if the rate of population growth is low, the loss of heterozygosity is substantial and time in generations at the low H is increased. A low rate of population growth in *S. olivaceus* may contribute to the low observed H. It is also possible that the rate of increase has been too rapid (due to increased adaptability) for the mutation rate to increase the average heterozygosity.

Data Set Congruence

Morphological evaluation of the 13 samples of *S. olivaceus* indicate that univariate meristic and morphometric basic statistics show random patterns of variation. Character state analyses reveal

no geographical affinities as well.

In general, multivariate analyses revealed little geographic differentiation between the samples. Trends, however, are evident in both morphometric and meristic characters of both sexes particularly in peripheral samples. Centroids for the four Texas samples (1-4) for male meristic characters tended to cluster along Vector I while the same samples for females tended to cluster along Vector II (see Figures 9 and 10). In males, sample 6 representing a valley population between Monclova and Cuatrocienegas, Coahuila tended to be separate along Vector I and II while for females sample 6 was not discriminated.

Sample 5 from near Nuevo Rosita, Coahuila, sample 6, and sample 7 from Huasteca Canyon, Nuevo Leon, and sample 4 from East Texas were discriminated along Vector I in the male morphometric analysis (Figure 11). In females, morphometric analysis revealed sample 8 from Linares and Santa Rosa Canyon, Nuevo Leon and sample 6 were discriminated along Vector II while samples 6 and 9 (northern Tamaulipas) were discriminated along Vector I (Figure 12).

Phenograms generated from both meristic and morphometric data for both sexes reveal some geographic affinities. Both male and female correlation phenograms distinguish the Texas samples; the remaining samples appear to cluster randomly. The distance phenograms for both sexes distinguish peripheral populations. In males, sample 8 and sample 12, the Juamave valley population, are distinguished from all others. In females, sample 6 is distinguished and samples 7 and 8 form a subcluster. The morphometric correlation

phenograms distinguish sample 8 in males and sample 7 in females while the remaining samples cluster randomly.

Allozyme data for *S. olivaceus* show patterns similar to the morphological data set. Two peripheral samples, 6 and 12, exhibit the highest distance values relative to the other samples. Further, phenograms based on matrices of Rogers genetic similarity (Figure 19) and Rogers modified distance (Figure 20) reveal similar patterns of geographic affinities. Both phenograms cluster Texas samples 1-4 with sample 5 and sample 7 with 8. The remaining clusters tend to exhibit randomness or non-geographic affinities. Peripheral samples 6 and 12 fall out in the Rogers modified distance phenogram.

Similarities between the morphological and allozymic data are apparent. In particular, samples 1-4 tend to cluster together and sample 6 tends to fall out in both data sets. One might conclude that the data sets are congruent. Dietz (1983) described permutation tests for association based on similarity or dissimilarity matrices. The Mantel test as described by Dietz is an unnormalized Pearson product-moment correlation coefficient which is dependent on the distance measure used. The test statistic used is $Z = X_{ij}Y_{ij}$ where X_{ij} and Y_{ij} are the geographic, taxonomic, or genetic distances between sample i and j. Mantel's test has been used to test spatial and temporal distances between disease cases (Mantel, 1967), evolutionary problems (Douglas and Endler, 1982), allele frequency differences and geographic distances (Jones *et al.*, 1980), and genetic and anthropometric distances (Spielman, 1973).

Dietz points out that Mantel's statistic is an unnormalized Spearman's rho correlation statistic (R) when using within-matrix ranks of the X_{ij}'s and Y_{ij}'s. Further, Kendall's tau approach may be applied to the distances with the test statistic $K = K_c + K_u$ with $K_c = \text{sign}((X_{ij} - X_{ik})(Y_{ij} - Y_{ik}))$ and $K_u = \text{sign}((X_{ij} - X_{kl})(Y_{ij} - Y_{kl}))$. Both K_c and K_u can be used as test statistics for congruency.

Dietz (1983) tested the power of the permutation tests. She found the K_c test to always be more powerful than the K_u test. Additionally, the K_c and R tests have similar power while the K_c test is almost as powerful as Z. Hubert (1978) noted the superiority of statistics (K_c) that incorporate with-in matrix comparisons over statistics (Z and R) that make between-matrix comparisons.

Mantel's test statistics (Z, R, K_c) were applied to male and female OTU distance, Roger's D, and geographic distance matrices for all pairwise comparisons to test for congruency. Table 25 summarizes these results. Male and female OTU distance matrices and female OTU distance and Rogers distance matrices are highly correlated (K =0.020 and 0.032, respectively) (P>0.95 level). All other comparisons are less correlated but above the P>0.90 level.

The Mantel's test indicates at least a tendency at the P>0.90 level for data set congruency in *S. olivaceus*. This suggests the possibility of a recent rapid range expansion such that the populations of *S. olivaceus* have not had time to accumulate sufficient differences. Further analysis of other species is needed ascertain the degree of congruency within the genus.

Table 25. Mantels test statistics for all pairwise comparisons of male and female OTU distances, Rogers D, and geographic distances. R=Spearmans rho correlation statistic, Z=Mantels test statistic, and K_c=Kendalls tau statistic. *=significant correlation (P 0.05).

	Female OTU	Rogers D	Geographic Distance
Male OTU	R=0.034 Z=0.012 K_c=0.020*	R=0.200 Z=0.180 K_c=0.098	R=0.178 Z=0.184 K_c=0.054
Female OTU	-	R=0.074 Z=0.014 K_c=0.032*	R=0.212 Z=0.214 K_c=0.086
Rogers D	-	-	R=0.192 Z=0.188 K_c=0.088

Interspecific Relationships

The taxonomic confusion between the *spinosus* and *undulatus* groups led Ferguson (1982) to study *S. cautus*, *S. olivaceus*, *S. undulatus*, and *S. exsul* in northeastern Mexico. Ferguson attempted to define the phenetic relationships of the four species and document the geographic range of and variation in *S. cautus* as well as determine the evolutionary history of the species. He notes that although there are karyotypic similarities between the four species, the morphological evidence suggests that the *undulatus* group probably did not evolve from the recent *S. cautus* missing link. He further proposed that *S. cautus* should be relegated to the *spinosus* group based on close morphological affinities with *S. olivaceus*.

Ferguson (1982) attempted to examine the possibility of intergradation between *S. cautus* and *S. olivaceus* by establishing transects from San Roberto to Linares, Nuevo Leon and from Tula to northwest of Ciudad Victoria, Tamaulipas. The San Roberto to Linares transect revealed that the two species appeared to be parapatric with marked ecological and morphological divergence between the two species with intergradation being unfounded. The Tula to Ciudad Victoria transect revealed that *S. olivaceus* was convergent with *S. cautus* such that the plausibility of intergradation existed.

An analysis of allozyme variation between *S. olivaceus*, *S. cautus*, and *S. spinosus* indicates that *S. cautus* is close to *S. olivaceus* and may belong to *spinosus* group. *S. spinosus* appears to be closer to *S. olivaceus*. Of the 17 loci examined, *S. spinosus* exhibited one fixed difference (PGM-2) with *S. olivaceus* while *S. cautus* exhibited three

fixed differences (ME, IDH, ADH). Phenograms produced by cluster analysis (UPGMA) of several algorithms depict *S. cautus* branching outside *S. spinosus* and *S. olivaceus*.

The distance Wagner tree procedure produces a tree forming an interconnected array of lineages. Internal nodes and branch lengths of the tree are positioned so the distance between all nodes is minimized such that observed distances are not greater than patristic distances. The polarity of the outgroup directed tree is based on the validity of the chosen outgroup and not on constancy of character evolution rates. The outgroup method is preferred as it negates the rate constancy assumption and OTU relationships can be better estimated. The distance Wagner tree (Figure 23) with *S. cyanogenys* as an outgroup depicts *S. cautus* clustering outside the *S. olivaceus* and *S. spinosus* cluster. *S. spinosus* clusters with samples 10 and 12 of *S. olivaceus* indicating that *S. olivaceus* is paraphyletic relative to *S. spinosus*. Patton and Smith (1981) note that electromorphic phylogenies at the population to species level are expected to reveal paraphyletic units in that electromorphic characters do not appear to be involved in any genetic revolution.

The preliminary evidence indicates that *S. spinosus* is closer to *S. olivaceus* than is *S. cautus*. This suggests the need for further analysis including all the species of both the *undulatus* and *spinosus* groups to better understand their relationships.

CONCLUSIONS

1. The range of karyotypic, electrophoretic, and morphological variation in *S. olivaceus* is narrow and indicates little geographic differentiation. Peripheral samples appear to be the most differentiatied.

2. Allozymic analysis of the populations of *S. olivaceus* reveals that the species is characterized by a large Ne. A low Fst value reflects a high level of gene flow between samples while low genetic distance values reveal little genetic differentiation, all indicative of large Ne species.

3. The low average heterozygosity value for *S. olivaceus* is a strong indication of a recent, past bottleneck or reduction in population size.

4. Morphological, genetic, and geographic distance data sets were found to be congruent at the 90% level of confidence indicating the probability of a recent rapid range expansion following the bottleneck; too rapid for populations to accumulate sufficient differences.

5. Interspecific relationships of the supposed close relatives of *S. olivaceus* indicate that *S. olivaceus* is paraphyletic relative to *S. spinosus*. *S. spinosus* appears closer to *S. olivaceus* than *S. cautus* while *S. cautus*, currently recognized as a member of the *undulatus* group, may be a member of the *spinosus* group.

LITERATURE CITED

Avise, J.C., and R.K. Selander. 1972. Evolutionary genetics of cave-dwelling fishes of the genus *Astyanax*. Evolution, 26:1-19.

Avise, J.C., M.H. Smith, and R.K. Selander. 1979. Biochemical polymorphism and systematics in the genus *Peromyscus*. VII. Geographic differentiation in the members of the *truei* and *maniculatus* species groups. J. Mamm., 60:177-192.

Baker, R.J., and J.W. Bickham. 1980. Karyotypic evolution in bats: Evidence of extensive and conservative chromosomal evolution in closely related taxa. Syst. Zool., 29:239-253.

Baker, R.J., M.W. Haiduk, L.W. Robbins, A. Cadena, and B.F. Koop. 1982. Chromosomal studies of South American bats and their systematic implications. *In*: Mammalian biology in South America (M.A. Mares and H.H. Genoways, eds.). Spec. Publ. Ser. Pymatuning Lab. Ecol., Vol. VI:303-327.

Benado, M., M. Aguilera, O.A. Reig, and F.J. Ayala. 1979. Biochemical genetics of chromosome forms of Venezuelan spiny rats of the *Proechimys guariae* and *Proechimys trinitatus* superspecies. Genetica, 50:89-97.

Bickham, J.W., and R.J. Baker. 1979. Canalization model of chromosomal evolution. Bull. Carnegie Mus. Nat. Hist., No. 13:70-84.

Blair, W.F. 1960. The rusty lizard, a populational study. Univ. Texas Press, Austin, 185 pp.

Bush, G.L. 1975. Modes of animal speciation. Ann Rev. Ecol. Syst., 6:339-364.

Bush, G.L., S.M. Case, A.C. Wilson, and J.L. Patton. 1977. Rapid speciation and chromosomal evolution in mammals. Proc. Nat. Acad. Sci., 74:3942-4946.

Bussjaeger, J.L. 1971. Phylogentic significance of the *spinosus* group of *Sceloporus* (Iguanidae). Ph.D. dissertation, University of Oklahoma, Norman.

Carpenter, C.C. 1967. Aggression and social structure in iguanid lizards. *In*: W.W. Milstead, Lizard ecology: a symposium. Columbia, Mo., Univ. Mo. Press. 300 pp.

Carpenter, C.C. 1973. Comparative behavior of the lizards in the genus *Sceloporus* (iguanids). Copeia, 1973(4):641-660.

Cole, C.J. 1970. Karyotypes and evolution of the *spinosus* group of lizards in *the* genus *Sceloporus*. Amer. Mus. Novitates, No. 2431:1-47.

Cole, C.J. 1971a. Karyotypes of the five monotypic species groups of lizards in the genus *Sceloporus*. Amer. Mus. Novitates, No. 2450:1-17.

Cole, C.J. 1971b. Karyotypes and relationships of the *pyrocephalus* group of lizards in the genus *Sceloporus*. Herpetologica, 27:1-8.

Cole, C.J. 1972. Chromosome variation in North American fence lizards (genus *Sceloporus*: *undulatus* species group). Syst. Zool., 24(4):357-363.

Cole, C.J. 1978. Karyotypes and systematics of the lizards in the *variablis*, *jalapae*, and *scalaris* groups of the genus *Sceloporus*. Amer. Mus. Novitates, No. 2653:1-13.

Cole, C.J., and C.R. Leavens. 1971. Chromosome preparations of amphibians and reptiles: improved techniques. Herpetol. Rev., 3:102.

Cope, E.D. 1900. The crocodilians, lizards, and snakes of North America. Ann Rept. U.S. Nat. Mus. for 1898:153-1294.

Davis, B.L., and R.J. Baker. 1974. Morphometrics, evolution, and cytotaxonomy of mainland bats of the genus *Macrotus* Gray (Chiroptera: Phyllostomatidae). Syst. Zool., 23:26-39.

Dietz, E.J. 1983. Permutation tests for association between two distance matrices. Syst. Zool., 32(1):21-26.

Douglas, M.E., and J.A. Endler. 1982. Quantitative matrix comparisons in ecological and evolutinary investigations. J. Theor. Biol., 99:777-795.

Farris, J.S. 1972. Estimating phylogentic trees from distance matrices. Amer. Nat., 106:645-668.

Ferguson, G.M. 1982. Distribution, variation, and phenetic relationships of the lizard *Sceloporus cautus* Smith in northeastern Mexico. MS thesis. Univ. Texas at El Paso. 195 pp.

Fitch, W.M., and E. Margoliash. 1967. Construction of phylogenetic trees, a method based on mutation distances as estimated from cytochrome c sequences is of general applicability. Science, 155:279-284.

Fritts, T.H. 1974. A multivariate evolutionary analysis of the Andean iguanid lizards of the genus *Sternocercus*. Mem. San Diego Soc. Nat. Hist., No. 7:1-86.

Gold, J.R. 1980. Chromosomal change and rectangular evolution in North American cyprinid fishes. Genet. Res., 35:157-164.

Gorman, G.C. 1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. pp. 349-424 *In* : Cytotaxonomy and vertebrate evolution (A.B. Chiarelli and E. Capanna, eds.). pp. 349-424, Academic Press, N.Y.

Gorman, G.C., and Y.J. Kim. 1975. Genetic variation and genetic distance among populations of *Anolis* lizards on two Lesser Antillean island banks. Syst. Zool., 24:369-373.

Gorman, G.C., Y.J. Kim, and C.E. Taylor. 1977. Genetic variation in irradiated and control populations of *Cnemidophorus tigris* (Sauria, Teiidae) from Mercury, Nevada with a discussion of genetic variability in lizards. Theor. Appl. Genet., 49:9-14.

Gorman, G.C., Y.J. Kim, and S.Y. Yang. 1978. The genetics of colonization: Loss of variability among introduced populations of *Anolis* lizards (Reptilia, Lacertilia, Iguanidae). J. Herpetol., 12:47-51.

Guttman, S.I. 1970. Hemoglobin electrophoresis in the iguanid genus *Sceloporus*. Comp. Biochem. Physiol., 34:563-568.

Hall, W.P. 1971. Chromosome evolution in the iguanid genus *Sceloporus*. Herpetol. Rev., 3:106.

Hall, W.P. 1973. Comparative population cytogenetics, speciation, and evolution of the iguanid lizard genus *Sceloporus*. Ph.D. dissertation, Harvard University. 193 pp.

Hall, W.P., and R.K. Selander. 1973. Hybridization of karyotypically differentiated populations in the *Sceloporus grammicus* complex (Iguanidae). Evolution, 27:226-242.

Hanks, B.G. 1983. The nature of electrophoretic variation in the lizards *Cnemidophorus gularis*, *C. inornatus*, *C. sexlineatus*, and *C. tigris*, with emphasis on populations from the Chihuahuan desert of Texas and Mexico. MS. thesis, Sul Ross State University. 102 pp.

Hubert, L.J. 1978. Generalized proximity function comparisons. Br. J. Math. Statist. Psychol., 31:179-192.

Hunsaker, D. 1962. Ethological isolating mechanisms in the *Sceloporus torquatus* group of lizards. Evolution, 16:62-74.

Iverson, J. B. 1977. Geographic variation in the musk turtle, *Sternotherus minor*. Copeia, 1977:502-517.

Iverson, J.B. 1979a. On the validity of *Kinosternon arizonense* Gilmore. Copeia, 1979:175-177.

Iverson, J.B. 1979b. A taxonomic reappraisal of the Yellow Mud Turtle, *Kinosternon flavescens* (Testudines: Kinosternidae). Copeia, 1979:212-224.

Jackson, J.F. 1973. Distribution and population phenetics of the Florida scrub lizard, *Sceloporus woodi*. Copeia, 1973:746-761.

Jones, J.S., R.K. Selander, and G.D. Schnell. 1980. Patterns of morphological and molecular polymorphism in the land snail *Cepaea nemoralis*. Biol. J. Linnean Soc., 14:359-387.

Kerster, H.W. 1964. Neighborhood size in the rusty lizard *Sceloporus olivaceus*. Evolution, 18:445-457.

Larsen, K.R. 1973. Speciation in the genus *Sceloporus* (Sauria, Iguanidae) as determined by cranial osteology and other characters. Ph.D. dissertation, Brigham Young University. 272 pp.

Larsen, K.R., and W.W. Tanner. 1974. Numerical analysis of the lizard genus *Sceloporus* with special reference to cranial osteology. Great Basin Nat., 34:1-41.

Larsen, K.R., and W.W. Tanner. 1975. Evolution of the sceloporine lizards (Iguanidae). Great Basin Nat., 35:1-20.

Larson, A. 1980. Paedomorphosis in relation to rates of morphological and molecular evolution in the salamander *Aneides flavipunctatus* (Amphibia, Plethodontidae). Evolution, 34:1-17.

Larson, A., and R. Highton. 1978. Geographic protein variation and divergence in the salamanders of the *Plethodon welleri* group (Amphibia, Plethodontidae). Syst. Zool., 27:431-448.

Lee, M.R. 1969. A widely applicable technique for direct processing of bone marrow for chromosomes of vertebrates. Stain Techn., 44:155-158.

Levin, D.A., and A.C. Wilson. 1976. Rates of evolution in seed plants: net increase in diversity of chromosome numbers and species numbers through time. Proc. Nat. Acad. Sci., 73:2086-2090.

Lowe, C.H., C.J. Cole, and J.L. Patton. 1967. Karyotypic evolution and speciation in lizards (genus *Sceloporus*) during evolution of the North American Desert. Syst. Zool., 16:296-300.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res., 27:209-220.

McKinney, C.O., R.K. Selander, W.E. Johnson, and S.Y. Wang. 1972. Genetic variation in the side blotched lizard (*Uta stansburiana*). Studies in Genetics VII, Univ. Texas Publ. No. 7213:307-318.

Nei, M. 1972. Genetic distance between populations. Amer. Nat., 106:283-292.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics, 89:583-590.

Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. Evolution, 29:1-10.

Nevo, E., Y.J. Kim, C.R. Shaw, and C.S. Thaeler, Jr. 1974. Genetic variation, selection and speciation in *Thomomys talpoides* pocket gophers. Evolution, 28:1-23.

Newman, H.H., and J.T. Patterson. 1909. Field studies of the behavior of the lizard *Sceloporus spinosus floridanus*. Bull. Univ. Texas Sci. Ser., 15:1-24.

Patton, J.L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae). J. Mamml., 48:27-37.

Patton, J.L., and J.H. Fedor. 1981. Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. Evolution, 35(5):912-920.

Patton, J.L., and M.F. Smith. 1981. Molecular evolution in *Thomomys*: Phyletic systematics, paraphyly, and rates of evolution. J. Mamm., 62(3):493-500.

Patton, J.L., and S.Y. Yang. 1977. Genetic variation in *Thomomys bottae* pocket gophers: macrogeographic patterns. Evolution, 37:697-720.

Penny, D.F., and E.G. Zimmerman. 1976. Genic divergence and local population differentiation by random drift in the pocket gopher genus *Geomys*. Evolution, 30:474-484.

Prager, E.M., and A.C. Wilson. 1975. Slow evolutionary loss of potential for interspecific hybridization in birds: a manifestation of slow regulatory evolution. Proc. Nat. Acad. Sci., 72:200-204.

Prager, E.M., and A.C. Wilson. 1976. Congruency of phylogenies derived from different proteins. A molecular analysis of the phylogenetic position of cracid birds. J. Mol. Evol., 9:45-57.

Purdue, J.R., and C.C. Carpenter. 1972a. A comparative study of the display motion in the iguanid genera *Sceloporus*, *Uta*, and *Urosaurus*. Herpetologica, 28(2):137-141.

Purdue, J.R., and C.C. Carpenter. 1972b. A comparative study of the body movements of displaying males of the lizard genus *Sceloporus* (Iguanidae). Behavior, 41:68-81.

Raff, R. A., and Kaufman. 1983. Embryos, genes, and evolution: the developmental-genetic basis of evolutionary change. McMillan Publ. Co., London. 395 pp.

Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Univ. Texas Publ. No. 7213:145-153.

Rohlf, F.J., and J. Kishpaugh. 1972. Numerical taxonomy system of multivariate statistical programs. The State Univ. of New York at Stony Brook, Stony Brook, N.Y. 87 pp.

SAS Institute, Inc. SAS User's Guide. 1979 Edition. SAS Institute, Inc., Cary, N.C., 1979. 494 pp.

Schmidly, D.F. 1973. Geographic variation and taxonomy of *Peromyscus boylii* from Mexico and the southern United States. J. Mamml., 54:111-130.

Schwartz, O.A., and K.B. Armitage. 1980. Genetic variation in social mammals: the marmot model. Science, 207:665-667.

Selander, R.K., D.W. Kaufman, R.J. Baker, and S.L. Williams. 1974. Genic and chromosomal differentiation in pocket gophers of the *Geomys bursarius* group. Evolution, 28:557-564.

Selander, R.K., M.H. Smith, S.Y. Yang, W.E. Johnson, and J.B. Gentry. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus* I. Variation in the old field mouse (*Peromyscus polionotus*). Studies in Genetics VI. Univ. Texas Publ. No. 7103.49-90.

Sites, J.W., Jr. 1980. Chromosome, allozyme, and morphometric variation in three cytotypes of the *Sceloporus grammicus* complex. Ph.D. dissertation, Texas A&M University. 121 pp.

Sites, J.W., Jr. 1982. Morphological variation within and among three chromosome races of *Sceloporus grammicus* (Sauria: Iguanidae) in the north-central part of its range. Copeia, 1982(4):920-941.

Sites, J.W., Jr. 1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus* I. Chromosome polymorphisms. Evolution, 37(1):38-53.

Sites, J.W., Jr., and J.R. Dixon. 1981. A new subspecies of the iguanid lizard, *Sceloporus grammicus*, from northeastern Mexico, with comments on its evolutionary implications and the status of *S. g. disparilis*. J. Herpetol., 15(1):59-69.

Sites, J.W., Jr., and J.R. Dixon. 1982. Geographic variation in *Sceloporus variablis*, and its relationship to *S. teapensis* (Sauria: Iguanidae). Copeia, 1982(1):14-27.

Sites, J.W., Jr., and I.F. Greenbaum. 1983. Chromosome evolution in the iguanid lizard *Sceloporus grammicus* II. Allozyme variation. Evolution, 37(1):54-65.

Sites, J.W., Jr., and M.W. Haiduk. 1979. The karyotype of *Sceloporus exsul* (Sauria: Iguanidae). Southwest. Nat., 24:393-395.

Smith, H.M. 1939. Mexican and Central American lizards of the genus *Sceloporus*. Bull. Field Mus. Nat. Hist., Zool., Ser. Vol. 26(245).

Sneath, P.H.A., and R.R. Sokal. 1973. Numrical taxonomy. W.H. Freeman Co., San Francisco. 573 pp.

Soule, M., and S.Y. Yang. 1973. Genetic variation in side-blotched lizards on islands in the Gulf of California, Mexico. Evolution, 27:593-600.

Spielman, R.S. 1973. Differences among Yanomama Indian villages: Do the patterns of allele frequencies, anthropometrics and map locations correspond? Am. J. Phys. Anthropol., 39:461-480.

Spohn, R.T., and S.I. Guttman. 1976. An electrophoretic study of inter- and intrapopulation genetic variation within the Northern Fence Swift, *Sceloporus undulatus hyacinthinus*. Comp. Biochem. Physiol., 55B:471-474.

Swofford, D.L., and R.B. Selander. 1981. Biosys-1: A Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Heredity, 72:281-283.

Templeton, A.R. 1980. Modes of speciation and inferences based on genetic distances. Evolution, 34:719-729.

Tinkle, D.W., and R.K. Selander. 1973. Age-dependent allozymic variation in a natural population of lizards. Biochem. Genet., 8:231-237.

Webster, T.P., R.K. Selander, and S.Y. Yang. 1972. Genetic variability and similarity in the *Anolis* lizards of Bimini. Evolution, 26:523-535.

White, M.J.D. 1968. Models of speciation. Science, 159:1065-1075.

White, M.J.D. 1969. Chromosomal rearrangements and speciation. Ann Rev. Genet., 3:75-98.

Wilson, A.C. 1976. Gene regulation in evolution. pp. 225-234. *In*: Molecular evolution, F.J. Ayala (ed.), Sinauer Associates, Inc., Sunderland, Mass. 277 pp.

Wilson, A.C., G.L. Bush, S.M. Case, and M.C. King. 1975. Social structuring of mammalian populations and rates of chromosomal evolution. Proc. Nat. Acad. Sci., 72:5061-5065.

Wilson, A.C., L.R. Maxson, and V.M. sarich. 1974a. Two types of molecular evolution. Evidence from studies of interspecific hybridization. Proc. Nat. Acad. Sci., 71:2843-2847.

Wilson, A.C., V.M. Sarich, and L.R. Maxson. 1974b. The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein, and anatomical evolution. Proc. Nat. Acad. Sci., 71:3028-3030.

Wilson, A.C., T.J. White, S.S. Carlson, and L.M. Cherry. 1977. Molecular evolution and cytgenetic evolution. pp. 375-393. *In*: Human cytogenetics: ICN-UCLA symposia on molecular and cellular biology. R.S. Sparkes, D.E. Comings, and C.F. Fox (eds,) Academic Press, New York.

Wright, S. 1931. Evolution in Mendelian populations. Genetics, 16:97-159.

Wright, S. 1978. Evolution and the genetics of populations. Vol. 4: Variability within and among natural populations. Univ. Chicago Press, Chicago.

APPENDIX A

SPECIMENS EXAMINED

Sceloporus olivaceus: TEXAS. KERR COUNTY. TCWC 129-130, 20.0 mi W Mt. Home TCWC 131-132, 5.0 mi W Hunt; TCWC 133, 3.0 mi S Kerrville; TCWC 456, Kerrville; TCWC 1105, 4.0 mi S Hunt; TCWC 4446, 40.0 mi W Kerrville; TCWC 18810-18814, Kerr Wildlife Area; KINNEY COUNTY. TCWC 437-439, 443, 5.0 mi E Bracketville; TCWC 35285, 22.9 mi E Del Rio; TCWC 60340-342, 20.0 mi E Del Rio, hwy 90; TCWC 60551, at Bracketville city limits; TCWC 60556, 7.1 mi W Bracketville; TCWC 60625-630, 6.0 mi E Bracketville, hwy 90; TCWC 60634-638, 3.4 mi S Bracketville, hwy 131; TCWC 60897-904, roadside park east of Bracketville, hwy 90; TCWC 62218, 37.0 mi N Eagle Pass on 279; TERRELL COUNTY. TCWC 444, 2.0 mi E Sanderson; TCWC 3991, 15.6 mi N Dryden; KU 2.0 mi SW Sheffield; MWSU 2032-033, 21.0 mi N Dryden; HASKELL COUNTY. Ku 176420, Haskell, ca. 20.8 mi SE; MWSU 2025, 6.0 mi E, 10.0 mi S Haskell; WICHITA COUNTY. MWSU 2026, Wichita Falls; MWSU 2045, 5.0 mi S Wichita Falls; DICKENS COUNTY. MWSU 2028, 1.0 mi E Dickens; GRAYSON COUNTY. MWSU 2034, 14.0 mi N Whitesboro; BAYLOR COUNTY. MWSU 2029, 17.0 mi E Seymour; MWSU 2030, 0.1 mi SW Seymour; MWSU 2044, 6.0 mi E View; LASALLE COUNTY. TCWC 338, 2.0 mi S Woodward; TCWC 339-340, 32.0 mi SE Cotulla; TCWC 341, Holland, Texas Dam; TCWC 14844, 5.0 mi S of Cotulla; TAIC 3646, 12.0 mi E of Encinal; BRAZOS COUNTY. TCWC 1042, 3.0 mi WNW Navasota; TCWC 7201, College Station; TCWC 14845, 10.0 mi S of Bryan; TCWC 15260, 1.0 mi N of College Station; TCWC 15444, 4.0 mi S College Station; TCWC

38725, Mussel Shoals; TCWC 51983, 2.5 mi W Texas A&M University, College Station; MSU-H 7878, 9.0 mi W of Bryan on Caldwell highway; MSU-H 7879, 6.0 mi WSW of Bryan of highway 21; YOUNG COUNTY. TCWC 1047, Jean. BOSQUE COUNTY. TCWC 1085, 5.0 mi W Norse; TCWC 18056, 9.0 mi N Kopperl; TCWC 18058, Bee Mts., 4.0 mi N Kopperl; TCWC 18059, Bee Mts., 6.0 mi N Kopperl; TCWC 60300-304, 1.9 mi N Meridian, hwy 144; TCWC 60308-315, hwy 144 at Walnut Springs; TCWC 60316, 3.0 mi N Clifton; TCWC 60317-322, 3.3 mi S Clifton; TCWC 60494-497, 2.5 mi N, 0.7 mi E Valley Mills; TAYLOR COUNTY. TCWC 2696, Lake Abilene; TCWC 60296-298, 60334, 60501-503, 3.1 mi SW Buffalo Gap; TCWC 60335-336, Buffalo Gap; SHSU 4285, Taylor Co.; MCLENNEN COUNTY. TCWC 2697, 4.0 mi W China Springs; TCWC 15209-210, Lake Waco; TCWC 15445, 2.0 mi W China Springs; TCWC 2775, 4.0 mi S China Springs; HAYS COUNTY. TCWC 2698, Taylor Ranch; TCWC 2699, 3.0 mi NE San Marcos; TCWC 8863, 1.0 mi N San Marcos; TCWC 8864, 1.0 mi W San Marcos; TCWC 18815, Wimberly; TCWC 23415, hillside near Masonic Temple, San Marcos; TCWC 23420-423, Hays Co.; TCWC 27233-239, 4.0 mi E of Wimberly; TCWC 14655, 31445, Fern Bank Springs on Blanco River; SHSU 2595, Hays Co.; ATASCOSA COUNTY. TCWC 2700-701, 8.0 mi SW Somerset; TCWC 5685, 1.0 mi E Pleasanton; TCWC 5688, Pleasanton; TCWC 62209, Cambellton; SHSU 4397, Atascosa Co.; WALKER COUNTY. SHSU 4998, Walker Co.; LEON COUNTY. SHSU 5217, 5222, Leon Co.; WILLACY COUNTY. SHSU 5219, Willacy Co.; DALLAS COUNTY. TCWC 4441, 9.0 mi W Dallas; TCWC 35284, 2.0 mi W Farmers Branch; BURNET COUNTY. TCWC 4442, 8.0 mi W Burnet; TCWC 60369-377, 0.5 mi W Bertram; TCWC 60827-828, 5.0 mi W Bertram, hwy

29; TCWC 61663, in Bertram; WILLIAMSON COUNTY. TCWC 4443-445, 4468, 1.0 mi E Granger; TCWC 60504-507, 1.0 mi W, 0.6 mi S Granger; TCWC 60550, 5.0 mi NW Georgetown; TCWC 60832, 5.0 mi SE Andice, CR 246; TCWC 61661, near Georgetown; SHSU 2059, Williamson Co.; EDWARDS COUNTY. TCWC 4447-448, 24.0 mi NE Rocksprings; TCWC 52201-204, 27.4 mi NW Rocksprings; TCWC 60624, 9.8 mi W Rocksprings, hwy 377; BROWN COUNTY. TCWC 4449, 4.0 mi SW Blanket; TCWC 14006, 10.0 mi S Bangs on hwy 586; KENEDY COUNTY. TCWC 4450, 4472-473, Norias, Armstrong; LIVE OAK COUNTY. TCWC 5675-676, 10.0 mi NW George West; TCWC 5687, George West; TCWC 10504-506, 20.0 mi SW Three Rivers; TCWC 60950-951, 22.7 mi NE Freer on 59; TCWC 60952, 7.8 mi SW George West on 59; TCWC 60953, 60891-892, 1.0 mi NE George West on 59; TCWC 60954, 11.0 mi NE George West on 59; TCWC 61044, 9.9 mi SW George West on 59; GILLESPIE COUNTY. TCWC 5677, 15.0 mi NE Fredericksburg; TCWC 5678, Fredericksburg; TCWC 60967, 62198, 4.0 mi N Fredericksburg, hwy 83; BREWSTER COUNTY. REO 426, Brewster Co.; PARKER COUNTY. TCWC 5679, 2.0 mi W Weatherford; TCWC 60477-486, 60489-493, 8.5 mi N Weatherford, hwy 180/80; TCWC 61676-678, 8.3 mi ENE Weatherford, Yarborough Farm; BAYUM 9509, 1.5 mi NW Aledo; BEXAR COUNTY. TCWC 5680, 5751, 1.0 mi W Helotes; TCWC 8865-866, NW side San Antonio; TCWC 12013, AMNH 7616, 7633-634, 37364-365, 44400, 46048-071, CAS-SU 31025-028 San Antonio; TCWC 14842-843, NW of San Antonio; SDNHM 46167-168, MTC, Fort Sam Houston; CAS-SU 31154-179, Leon Springs; SHSU 5411, Bexar Co.; EASTLAND COUNTY. TCWC 5681-682, 3.0 mi N Ranger; VAL VERDE COUNTY. TCWC 5683, 10.0 mi NW Del Rio; TCWC 54070, Amistad Nat'l. Recreation

Area, at Long Point; TCWC 60874, 2.0 mi S Juno, hwy 163, near Johnson's Pass; TCWC 60885, 60887-889, 60894-895, 26.6 mi N Langtry, Everett's Crossing; TCWC 60890, 14.8 mi NW Del Rio, Amistad Lake; TCWC 60893, Amistad Lake, under hwy 90 bridge; TCWC 60896, north edge of Langtry on road to Everett's Crossing; TAIC 742, near Comstock on U.S. 277; TAIC 2489, Caulk Ranch; TAIC 3363.1-363.2, Pandale rd crossing of Pecos River; TAIC 4428.1-428.2, 1.0 mi SE Del Rio; TAIC 4478.1-478.3, 25.0 mi N of Langtry, Everetts Crossing TAIC 4789, Pandale Road; TAIC 4800.1-800.3, 4839.2, Everetts Crossing; KU 11722-724, nr. mouth of Devil's River; KU 12638, mouth Pecos River; MWSU 2041, 20.0 mi S Juno; TRAVIS COUNTY. TCWC 5684, 15072, 60339, Austin;♀ SHSU 1680, 26.0 mi NE Austin; UPTON COUNTY. SHSU 2399, Upton Co.; JIM WELLS COUNTY. TCWC 5686, Corpus Christi Lake; TCWC 38723, 3.4 mi W jct fm rd 624 and U.S. hwy 281; TAIC 294, 3.5 mi NW of Alice; TARRANT COUNTY. TCWC 5689, MWSU 2031, Fort Worth; TCWC 18820, Clear Fork of TRinity River, 10.0 mi SW Fort Worth; TCWC 20344-345, Arlington; TCWC 23416-419, 2.0 mi W TCU Campus, Edward's Ranch, Trinity River Clear Fork; TCWC 61651-657, S of Whites Settlement in Fort Worth near IH 30; CAMERON COUNTY. TCWC 5690, 8867-869, 14004-005, AMNH 9420, 22985-986, Brownsville; TAIC 2514.1-514.1, 5.0 mi SE of Brownsville; TAIC 4034, Southmost Ranch, 5.0 mi SE of Brownsville; MWSU 2042, 0.5 mi W Harlingen; NUECES COUNTY. AMNH 1364-365, Corpus Christi; AMNH 8159, Padre Island; TAIC 63, 65.1-65.2, jct of Texas hwy 286 and Oso Creek; TAIC 64.1-64.3, 1.0 mi NW Bluntzer Ranch, Nueces River; TAIC 70, 5.0 mi N of Robstown; TAIC 231, 6.0 mi SE of Agua Dulce; ANDERSON COUNTY.

TCWC 5782, 20.0 mi NW Palestine; BAYUM 11995-996, 10.0 mi S Palestine; BASTROP COUNTY. TCWC 10507, 2.5 mi NW Smithville; TCWC 31004, end of ranch road 2430; TCWC 31446, 1 mi W Cedar Creek; TCWC 62217, 4.7 mi S Smithville on 95; STARR COUNTY. TCWC 13210, Starr Co.; TCWC 51834, Falcon Heights; TCWC 60970, 2.0 mi E La Gloria, hwy 755; TCWC 60979-980, 5.3 mi SW La Gloria, hwy 755; TCWC 60981, 1.4 mi W La Gloria, hwy 755; TCWC 60990, 11.7 mi SW La Gloria, hwy 755; TCWC 62199, 3.1 mi N Sullivan City; TCWC 62200, 3.4 mi N Sullivan City; TCWC 62201, 1.9 mi W Sullivan City; TCWC 62202-204, 6.1 mi W Sullivan City on 83; SAN SABA COUNTY. TCWC 13799, 1.0 mi S Bend; ERATH COUNTY. TCWC 14003. 3.0 mi NW Stephenville; FALLS COUNTY. TCWC 14840. 5.0 mi WNW of Chilton; TCWC 60871-873, 4.4 mi NW Reagan, hwy 6; TCWC 61659, 5.0 mi SE Marlin on hwy 6; HILL COUNTY. TCWC 14841, near Lake Whitney Dam; TCWC 29051, 5.0 mi W of Covinton on hwy 67; BANDERA COUNTY. TCWC 15207,15440, 10.0 mi SW of Medina; TCWC 15000, 15208, 9.0 mi W of Medina; TCWC 15442, Buchanan Ranch; TCWC 35286, 8.0 mi SW Medina; CORYELL COUNTY. TCWC 15211, 15441, 5.0 mi SW Moshiem; TCWC 60866-869, 6.7 mi E Evant, hwy 84; TCWC 60870 8.2 mi E Gatesville; COMANCHE COUNTY. TCWC 15259, 2.0 mi NW De Leon; TCWC 60498-500, 1.0 mi SE Gustine, hwy 36; LLANO COUNTY. TCWC 15356, W.J. Williams Ranch; TCWC 60388-389, ca. 1.0 mi W Buchanan Dam, jct hwys 29 and 261; TCWC 60394, 12.9 mi W Llano, hwy 29; TCWC 60395, 4.3 mi W Llano, hwy 29; TCWC 60815-822, 60830-831, 23.0 mi S Llano, FM 2323; TCWC 60833-835, 60966, 61648, 5.0 mi S Llano, hwy 16; TCWC 61664, 10.8 mi E Llano; TCWC 61665, 3.1 mi E Llano; TCWC 61666, 4.7 mi WNW Llano; TCWC 61667, 6.3 mi

WNW Llano; HIDALGO COUNTY. TCWC 18050-502, McAllen; TCWC 18055, Sharyland Rd., 2.5 mi S of hwy 83; TCWC 18059, FM 1926, 0.5 mi N Hidalgo; TCWC 21159, 1/8 mi N Shuryland Rd, 1/8 mi W of Mission; TCWC 27766, 4.0 mi N La Joya; TCWC 36521-522, 13.0 mi N Edinburg, La Coma Ranch; TCWC 54470, Santa Ana NWR; TCWC 54471, 3.0 mi S Mission in Bentsen; TCWC 54592-594, 8.0 mi S Alamo; TCWC 61662, 2.0 mi S, 3.7 mi E Hidalgo; TAIC 2945, McAllen City Limits; MWSU 2039, 5.0 mi E Hidalgo; MONTAGUE COUNTY. MWSU 2035, 8.0 mi SW BOWIE; MWSU 2043, 8.0 mi S St. Jo; MWSU 4074, 5.6 mi NE Nacona; COLEMAN COUNTY. TCWC 18816, 18818-819, Day Ranch, 22.0 mi S Valera; TCWC 23413-414, Colorado R. between Coleman and Concho Counties; PALO PINTO COUNTY. TCWC 18817, 2.0 mi SW Bennet; TCWC 25283, 25285-286, BSA Camp Constantin; TCWC 25284, near Morris Shepard Dam; TCWC 61683, east side Possum Kingdom Lake; MWSU 2027, 3.0 mi S Mineral Wells; MWSU 2046, 2.0 mi NW Grayford; GOLIAD COUNTY. TCWC 20185-187, 1.0 mi NE of Goliad, hwy 59; TCWC 51980-981, 3.5 mi N Goliad; TCWC 60957, 61057, 2.8 mi N Goliad; AMNH 46072-076, Charco; CALDWELL COUNTY. TCWC 20271, 1.0 mi W U.S. hwy 183, 7.0 mi N Lockhart; COLORADO COUNTY. TCWC 20392, SW of Eagle Lake; BELL COUNTY. TCWC 20393, Belton area; TCWC 23068, Tample; TCWC 23069, 0.3 mi W intersect. St. hwys 317 and 36, Cedar Creek at hwy 36 bridge; TCWC 23070, 5.1 mi SW intersect. St. hwy 190 and FM 1670, Stillhouse Hollow Dam; TCWC 27240, 1514 S 37th in Temple; UVALDE COUNTY. TCWC 20767, 8.0 mi W of Sabinal; TCWC 21158, pavilion at Garner State Park; TCWC 44159, 8.0 mi N Uvalde; TCWC 48133-134, 7.8 mi N of jct hwys 83/90, near hwy 90; TCWC 48161, ca. 8.0 mi N Uvalde, on hwy 83, Leona

River; TCWC 49109-127, 49129, 51198, 13.0 mi N Uvalde, jct 93/90, David Gulley Ranch; TCWC 60343, 24.2 mi E Bracketville, hwy 90; TCWC 60972-974, in Uvalde; TCWC 62075, 62197, 7.8 mi N Uvalde, hwy 83; NAVARRO COUNTY. TCWC 22235, mixing room of Collin St. Bakery, Corsicana; KLEBERG COUNTY. TCWC 22541, hwy 77 and SFR rd. 771; TCWC 35288-290, Riviera; TAIC 61.1-61.3, 8.0 mi SE of Ricardo; TAIC 68.1-68.2, 7.3 mi E of U.S. 77 of FM 772; TAIC 69, caught in N216, Texas A&I, Kingsville; TAIC 198.1-198.2, 200, 1.0 mi N of Vattman; TAIC 199, 2.0 mi S of Ricardo; TAIC 271, 1230 W. Santa Getrudis; TAIC 522.1-522.2, Kingsville city limits; TAIC 530, A&I south pasture; BEE COUNTY. TCWC 18053-054, Segar Ranch, 5.5 mi S Beeville; TCWC 31000, in Skidmore; TCWC 60955, 7.0 mi WSW Beeville on 59; TCWC 60956, 4.3 mi WSW of Beeville on 59; CONCHO COUNTY. TCWC 23412, 14.5 mi W Miller's View; TCWC 61669, 9.4 mi E Eden; HOOD COUNTY. TCWC 18076-077, 1.0 mi E Granbury, along Brazos River; TCWC 25262, 0.5 mi SE Lipon; TCWC 25264, 14.0 mi S of Lipon; BAYUM 11994, 1.5 mi SE Granbury; BAYUM 10677, 2.0 mi N Granbury; SHSU 2828, Hood Co.; WALLER COUNTY. BAYUM 8220, hwy 290; MASON COUNTY. TCWC 30997, 10.0 mi S of Mason; TCWC 30998, 9.0 mi SW of Mason; TCWC 30999, 9.0 mi S of Mason; TCWC 60362, 60823, Mason, Mason Co. Park; TCWC 60380-382, 4.0 mi W Mason, jct hwys 29 and 377; WASHINGTON COUNTY. TCWC 31001, 3 3/4 mi S of Burton; TCWC 31002, Mayfair Ranch; COOKE COUNTY. TCWC 31003, 5.5 mi SE of Gainsville; KU 12641, nr Gainsville; MWSU 2038, 8.0 mi W Gainsville; BROOKS COUNTY. TCWC 35287, Brooks Co.; TCWC 60968, 17.3 mi W Rachal, hwy 755; TCWC 60969, 19.4 mi W Rachal, hwy 755; TCWC 60971, 1.4 mi W

Rachal, hwy 755; MCMULLEN COUNTY. TCWC 36580, 8.0 mi W Whittset; TCWC 48641, 15.0 mi NE Tilden, Brown Division Buena Vista Ranch; TCWC 60948, 19.5 mi NE Freer on 59; TCWC 60949, 22.2 mi NE Freer on 59; TCWC 62206-208, Tilden Lions Rodeo Grounds, jct 17/16; MENARD COUNTY. TCWC 37992, 3.0 mi E Menard, ∪÷FM road 2092; TCWC 37993, Menard city limits; TCWC 60378, 60829, 4.1 mi W Hext, hwy 29; TCWC 60396, 14.4 mi S Menard, hwy 83; KIMBLE COUNTY. TCWC 38724, 2.0-4.0 mi N Cleo; TCWC 60379, London, hwy 377; TCWC 60390-391, Junction; MWSU 2049-050, 10.0 mi E Junction; BAYUM 11263, 6.1 mi N Junction; WISE COUNTY. MWSU 2047-048, 3.0 mi WNW Bridgeport; BAYUM 9510, nr. Boyd; CLAY COUNTY. MWSU 2051-052, Blue Grove; DENTON COUNTY. BAYUM 9511, 10.0 mi MW Krum; COMAL COUNTY. TCWC 46504, Potters Creek Park; TCWC 60352, Canyon Lake Dam; BLANCO COUNTY. TCWC 60363, 7.4 mi N Johnson City, hwy 281; TCWC 51982, 2.5 mi N Johnson City; MILAM COUNTY. TCWC 60366-368, 60824-826, 6.0 mi SW Rockdale, hwy 79; LEE COUNTY. TCWC 41835, Manheim, hwy 21 roadside park; TCWC 60997-002, 6.0 mi WSW Lincoln, hwy 21; MEDINA COUNTY. TCWC 49108, 1.0 mi S D'Hanis; TCWC 60344-345, 6.2 mi W D'Hanis; TCWC 60346-351, 60877, 60996, 3.1 mi W D'Hanis, hwy 90; TCWC 60631-633, 27.0 mi S San Antonio, I-35; TCWC 60975-978, 6.6 mi W D'Hanis roadside park; MAVERICK COUNTY. TCWC 49128, 23.0 mi SE Bracketville, TAMU Rio Grande Exp. Ranch; TCWC 60879, 34.0 mi NNW Eagle Pass, hwy 277; TCWC 60880-882, 36.8 mi NNW Eagle Pass, hwy 277; TCWC 60883-884, 38.3 mi NNW Eagle Pass, hwy 277; TCWC 60985-986, 5.0 mi NNW Eagle Pass, hwy 277 Elm Creek; TCWC 60987, 6.0 mi NNW Eagle Pass, hwy 277; TCWC 60991-993, 27.1 and 28.3 mi NNW Eagle Pass, hwy 277; TCWC

60994-995, 31.0 mi NNW Eagle Pass, hwy 277; TCWC 61003-005, 32.3 mi NNW Eagle Pass, hwy 277; TAIC 747.1-747.3, 1.0 mi E of Eagle Pass, U.S. 277; KU 15313, Eagle Pass; JIM HOGG COUNTY. TCWC 49328, 13.7 mi N Guerrera, hwy 649; REFUGIO COUNTY. TAIC 2873.1-873.2, 1.0 mi E of jct 113 and 35; SOMERVELL COUNTY. TCWC 58414-415, 60016, 7.0 mi NW Glen Rose; TCWC 60305-307, 2.2 mi N jct hwys 144 and 67 on 144; FRIO COUNTY. TCWC 57012, 3.0 mi S, 3.5 mi W Pearsall; BAYUM 5050-051, Pearsall; REAL COUNTY. BAYUM 5129, 5174-175, Real Co.; ZAPATA COUNTY. TCWC 57019, Zapata, Swantner-Hunter Ranch; TCWC 62205, 2.2 mi N Zapata on 83; BAYUM 5765, Falcon Lake; BAYUM 5766, 2.5 mi N Falcon; JEFFERSON COUNTY. BAYUM 5976, Jefferson Co.; HEMPHILL COUNTY. BAYUM 5977, 3.0 mi NE Briscoe; SAN PATRICIO COUNTY. BAYUM 5992, near Raft; SMITH COUNTY. BAYUM 5963, 10.0 mi N Tyler; SUTTON COUNTY. TCWC 60383-386, 7.0 mi W Sonora, I-10; STONEWALL COUNTY. TCWC 60837, 5.7 mi W Aspermont, hwy 380; TCWC 60838, 10.7 mi W Aspermont, hwy 380; KENT COUNTY. TCWC 60839, 4.3 mi E Clairmont, hwy 380; TCWC 60840-843, 4.3 mi W jct hwys 380/208 on 380; IRION COUNTY. TCWC 60844, 5.2 mi W Mertzon, hwy 67; TCWC 60845-850, 3.5 mi W Mertzon, hwy 67; TCWC 60851-857, in Mertzon on hwy 67; MCCULLOCH COUNTY. TCWC 60858, 13.0 mi E of Doole in Fife, hwy 765; TCWC 61668, 2.2 mi W Voca; MILLS COUNTY. TCWC 60859-865, Mills Co. Park in Goldthwaite; WEBB COUNTY. TCWC 60878, 38.5 mi N Laredo, hwy 83, at the Oasis Bar; TCWC 60886, 30.1 mi N Laredo, hwy 83; TCWC 60938, 2.7 mi S La Salle/Webb Cos. line, IH-35; TCWC 60982-983, 11.7 and 14.0 mi N Laredo, hwy 83; TCWC 60894, 20.6 mi N Laredo, hwy 83; TCWC 61006, 48.6 mi N Laredo, hwy 83; TCWC 61007,

21.6 mi N Laredo, hwy 83; TAIC 730, jct 44 and 83; TAIC 2167, 3.0 mi NW jct 44 and 83 on 83; TAIC 2370, 10.0 mi W of Freer on hwy 44; TAIC 3648.1-648.2, Oasis Bar jct of hwy 44 and U.S. 83; KU 12639, Laredo; KU 50676, 10.0 mi NNW Laredo Islitas; KU 126991-992, 40.0 mi WNW Laredo on hgwy 1472, Trevino Ranch; KU 126993, 43.0 mi S Carrizo Springs, 4.0 mi W jct hgwys 83 and 44; DUVAL COUNTY. TCWC 60947, 18.3 mi NE Freer on 59; TCWC 61660, La Capita Ranch; TAIC 4266, 5.0 mi SE of Benavides on FM 2295; DEWITT COUNTY. TCWC 60958, 8.3 mi S Cuero; TCWC 60959-960, 4.7 mi S Cuero; TCWC 60961-965, Cuero City Park; DIMMIT COUNTY. TCWC 60988-989, Little League Park in Carrizo Springs; TAIC 71, 7.1 mi E of Catarina; KU 11707-712, near Carrizo Wells, Nueces River; ARCHER COUNTY. TCWC 61650, near water plant at Lake Kickapoo' MWSU 2040, 2087, 12.0 mi N Archer City; MWSU 2036, 16.0 mi NNE Archer City; MWSU 2057, 2059-060, 2065, Lake Kickapoo; MWSU 2058, 10.0 mi NE Archer City; MWSU 2062, 14.0 mi N Archer City; MWSU 2063, 5.0 mi S Archer City; MWSU 2066, 4.0 mi NW Archer City; MWSU 2061, 7.0 mi S Winthorst; MWSU 2064, 3.0 mi S Winthorst; MWSU 2067, Kickapoo spillway; JACK COUNTY. TCWC 61658, 2.4 mi NW Jacksboro on 281; MWSU 2054, 2056, 1.0 mi NE Jacksboro; MWSU 2053, 2055, 5.0 mi NE Jacksboro; BAYUM 9507-508, 5.0 mi NW Perrin; COKE COUNTY. TCWC 61670, 8.3 mi S Robert Lee; MITCHELL COUNTY. TCWC 61671, 10.0 mi S, 1.0 mi W Colorado City; GARZA COUNTY. TCWC 61672-674, 9.0 mi SE Post; TCWC 61675, 5.3 mi NE Post on 651; ELLIS COUNTY. TCWC 61679, 4.4 mi ENE Italy; CROSBY COUNTY. TCWC 61680, 0.4 mi E 651/2794 on 2794; THROCKMORTON COUNTY. TCW 61681-682, 4.4 mi E Throckmorton; KU 61685, 19.0 mi NW Albany; TOM

GREEN COUNTY. KU 88182-183, Knickerbocker; KU 88184, W edge San Angelo; CROCKETT COUNTY. KU 88185, Pecos River E Sheffield; BAYUM 9504, nr. Ozona; KARNES COUNTY. TCWC 62210, 0.4 mi NE Falls City; TCWC 62211, jct 123/887; WILSON COUNTY. TCWC 62212, 1.4 mi N Wilson/Karnes Cos. line on 80; GONZALES COUNTY. TCWC 62213, 2.4 mi NE jct 80/97 on 97; TCWC 62214, 4.7 mi NE jct 80/97 on 97; TCWC 62215-216, 2.9 mi SW Cost on 97. CAS-SU 18109, Palmetto State Park. OKLAHOMA. LOVE COUNTY. KU 15024-026, near Marietta. NEW MEXICO. BAYUM 5766, 6.0 mi S Las Cruces, Rio Grande River. MEXICO. TAMAULIPAS. TCWC 6954, 1.0 mi NE Padilla; TCWC 26482, 18.0 mi E Cd. Mante; TCWC 26483, 15.0 mi E Cd. Mante; TCWC 39654, 7.6 mi S Nuevo Padilla at Rio Corona; TCWC 48136, Rio Carrizal, 48.0 mi S Soto La Marina; TCWC 49530, 2.0 mi W Rancho Carricitos; TCWC 49531, 0.5 mi W Rancho Carricitos; TCWC 49532, 0.3 mi SSW Rancho Carricitos; TCWC 49533, 1.1 mi E Tinaja; TCWC 49534, 2.2 mi S Gavilan; TCWC 49535, 0.7 mi S Gavilan; TCWC 49536-539, 0.3 mi W Rancho Carricitos; TCWC 49540-541, 0.2 mi W Union Morales; TCWC 49542-543, 2.6 mi WNW San Carlos; TCWC 55035, 6.0 km W Marmelejo; TCWC 58112, 3.1 mi SE San Carlos; TCWC 60906-907, 3.0 mi NNW San Carlos; TCWC 60908, 1.5 mi N Ejido Correlejo; TCWC 60909-914, 16.6 mi E jct 85 and 180 in Victoria; TCWC 60915, 0.3 mi W Soto La Marina; TCWC 60916-927, 4.8 mi S Soto La Marina; TCWC 60928-930, 36.6 mi S Soto La Marina; TCWC 60931, 1.0 mi SW Aldama; TCWC 60932, 7.3 mi W Marvel on 80; TCWC 60933-936, 3.0 mi N of Juamave on 101; TCWC 60937, 7.1 mi W Linares on 60(58); SDNHM 52732, 9.0 mi E Juamave; KU 35060-061, MSU-H 4313, Soto La Marina; KU 61683-684, 3.0 mi SW Ciudad Victoria; KU

68102-104, San Fernando; KU 68105, 2.0 mi W San Fernando; BAYUM 8203, 6.8 mi E Xicotencatzl; BAYUM 8219, Tamaulipas; MSU-H 4312, 7.0 mi W La Pesca; NUEVO LEON. TCWC 909, Rio Ramos, 20.0 km NW Montemorelos; TCWC 16978, 2.0 mi E Santiago; TCWC 43883, 13.2 mi SE Soledad; TCWC 43884, 19.2 mi SW Mina; TCWC 49644, 4.7 mi SSE Santa Catarina; TCWC 51618, 51692, Cuesta Mamulique, 19.2 mi N Cienega de Flores; TCWC 51693, 5.5 mi SSE Santa Catarina in Huasteca Canyon; TCWC 51782, 3.8 mi SSE Santa Catarina in Huasteca Canyon' TCWC 53930, 18.2 mi (rd) WSW Linares on St. hwy 60; TCWC 57294, 3.5 mi W Sabinas Hidalgo, Ojo de Agua; TCWC 60940, 18.0 mi E Linares in Linares Canyon; TCWC 60941-942, 19.8 mi S Sabinas Hidalgo; TCWC 60943, 16.0 mi W Sabinas Hidalgo; TCWC 60944-946, 2.1 mi W Sabinas Hidalgo (Ojo De Agua); TCWC 61030-031, 1.0 mi S Morelos; TCWC 61032, 12.1 mi W jct hwys 53/40 Monterrey bypass; TCWC 61033-038, 5.3 mi S Santa Catarina; TCWC 61039-040, 3.1 mi S Santa Catarina; TCWC 61041-042, 18.0 mi W Linares on 60; TCWC 61043, 7.7 mi W Linares; TCWC 61056, 19.8 mi S Sabinas Hidalgo; KU 33595, 38093, 7.0 mi S, 16.0 mi W Linares; KU 92604-605, La Boca; KU 128834, 24.9 km NW La Gloria on Anahuac-La Gloria road; BAYUM 8210, 50.0 mi SE Monterrey; COAHUILA. TCWC 43885, 1.2 mi S Santa Teresa; TCWC 43886, 19.1 mi E Casa Colorados; TCWC 46783, 2.8 mi NE Sacramento; TCWC 46784, 2.6 mi WSW La Madrid; TCWC 46785, 1.0 mi W Hermanas; TCWC 46786-787, 25.9 mi N Hermanas; TCWC 49546, 6.7 mi W Sacramento; TCWC 60939, 2.7 mi SSE Buenaventura; TCWC 61008, 22.0 mi S Piedras Negras; TCWC 61009, 13.7 mi N Nueva Rosita; TCWC 61010, 13.1 mi N Nueva Rosita; TCWC 61001, 8.8 mi N Nueva Rosita; TCWC 61012-013, 1.0 mi N Nueva Rosita;

TCWC 61014-015, 2.7 mi SSE Buenaventura; TCWC 61016-020, 1.6 mi W Celemania; TCWC 615, 1.6 mi E Celemania; TCWC 61026-029, 2.4 mi E Celemania; KU 33593-594, La Gaches; KU 38173-174, 4.0 mi NE Ocampo; KU 38177, 16.0 mi E, 18.0 mi N Ocampo; KU 38320, 4.0 mi N Las Margaritas; KU 39888, 12.0 mi N, 12.0 mi W Jimemez; KU 128832-833, S end Don Martin Dam, Hotel Club Deportiva; KU 28099, 6.0 mi SW San Geronimo;

Sceloporus cautus. MEXICO. NUEVO LEON. TCWC 61066-071, 61073-084, RHD 1365-1-8, 6.1 mi E San Roberto TCWC 61085, 15.3 mi E San Roberto on 60; TCWC 61086-088, 12.7 mi W Iturbide on 60;

Sceloporus cyanogenys. TEXAS. STARR COUNTY. TCWC 62220-221, 1.9 mi W Sullivan City on 87 TCWC 62222-229, 6.1 mi W Sullivan City on 83; ZAPATA COUNTY. TCWC 62230-232, 6.7 mi NW Zapata on 83; TCWC 62233-235, 7.2 mi NW Zapata on 83; MEXICO. NUEVO LEON. TCWC 61112, Mamaulique Pass, 23.2 mi S Sabinas Hidalgo;

Sceloporus spinosus. MEXICO. NUEVO LEON. TCWC 61049, 10.4 mi E San Roberto on 60 TAMAULIPAS. TCWC 61047, 11.0 mi N SLP border on 101; TCWC 61048, at Palmillas on 101; QUERETARO. TCWC 60799-801, 1.9 mi N of Antongo-Colon road; TCWC 60802, Jct. Cues/Galindo Queretaro road; TCWC 60803, 4.5 mi E Pena Miller; TCWC 60804, 13.9 mi E jct hwy 120 and road to Vista Hermosa.